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Oxic and anoxic decomposition of tubes from the burrowing sea anemone *Ceriantheopsis americanus:* Implications for bulk sediment carbon and nitrogen balance

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ABSTRACT

Many marine infaunal animals form organic tube and burrow linings. The role of these materials in organic matter cycling and preservation in sediments is largely unknown. In the case examined here, the infaunal sea anemone, *Ceriantheopsis americanus,* (a common component of bottom communities along the east coast of North America) forms a leathery, fibrous tube lining 2–3 mm thick, ~1 cm in diameter, and typically extending 20–30 cm into deposits. Tube fibers (~2 mm long, 2–5 μm thick) formed from discharged specialized nematocyst cells, ptychocysts, are composed of a silk-like protein copolymer, cerianthin. Tubes incubated under oxic and anoxic conditions over a period of 122 days demonstrate that initial rates of whole tube decay are 10–100 times slower than usually found for fresh planktonic debris and aquatic macrophytes despite a relatively low molar C:N ratio of ~5.1. First order decomposition rate constants in oxic water, anoxic water and anoxic sediment are ~0.76, ~0.41 and ~0.22 yr^{-1} for particulate tube carbon and ~0.2, ~0.1 and ~0.1 yr^{-1} for particulate nitrogen, respectively (20°C). There are no obvious (under SEM) morphological changes in tube fibers during initial tube decomposition, implying slower long term rates. Although slow, tube decomposition stimulates bacterial activity in sediments from below ~10 cm depth where any organic matter present is even more refractory than the tubes themselves. In central Long Island Sound muds, tubes apparently account for a minimum of ~0.6–1.8% and 2.8–8.4% of the steady state C and N detrital pools in the upper 10–30 cm of the sediment. *C. americanus* tube production apparently accounts for ~9% of the average particulate carbon and ~12% of the nitrogen fluxes to the benthos. Tube construction by infaunal benthos may thus represent an important pathway for refractory compound formation and organic matter preservation.

1. Introduction

The presence of biogenic structures, such as tubes and burrows formed by bottom-dwelling animals, may significantly affect physical, chemical and biological characteristics of a sedimentary deposit (e.g. Rhoads, 1974; Aller, 1982; 1988; Krantzberg, 1985; Kristensen, 1988). Many studies have shown that benthic animals

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generally stimulate transport and reaction rates in bioturbated sediments relative to sediments with few infauna. The *direct* animal contributions to the transformation and mineralization of organic matter in sediments, by feeding, excretion and tube formation, are less well described. For example, the protein rich mucopolysaccharide secretions produced by most infaunal animals during burrow and tube formation are usually considered a readily degradable substrate for microbial growth (Kristensen *et al.,* 1985; Aller and Aller, 1986; Reichardt, 1988). However, burrow or tube structures formed by various infaunal species may differ in appearance, composition and function. They can be mucoid, membranous, encrusted with sand or shell debris, horny or calcareous, etc. (Defretin, 1971). The biodegradability of tubes may be highly dependent on the chemical composition and structure of the secreted material. Considering the abundance of benthic infauna in most coastal marine sediments, the formation and decay of more or less stable burrow or tube structures may contribute significantly to overall detritus dynamics.

The present work focuses on decay characteristics of tubes from the infaunal sea anemone *Ceriantheopsis americanus. C. americanus* lives in sandy and silty sediments underlying relatively quiet, shallow waters along the east coast of North America. The typically 5–10 cm long animals line 10–30 cm deep vertical, unbranched burrows with very strong and flexible tubes composed of protein rich fibers mixed with sedimentary particles (Mariscal *et al.,* 1977; Bishop *et al.,* 1978). The upper few centimeters of the tubes can protrude above the sediment into the overlying water, but are often flush with the sediment-water interface in subtidal Long Island Sound (Fig. 1). *C. americanus* feeds by trapping plankton and detritus particles from the overlying water using its tentacular crown, or by capturing small macrofauna and meiofauna at the sediment surface (D. Rudnick, pers. comm.; Eleftheriou and Basford, 1983).

Our experimental approach was to compare decomposition patterns of freshly collected tubes (1) exposed to oxic sea water, (2) exposed to anoxic sea water, or (3) buried in anoxic sediment. Tube decay was followed using changes in particulate and soluble carbon, nitrogen and sulfur pools and the activity level and density of tube-associated bacteria. The role of *C. americanus* tubes for overall detrital carbon and nitrogen balance in central Long Island Sound muds was also evaluated.

2. Materials and methods

a. Tube collection

Tubes of *C. americanus* used in the decomposition experiments were collected from muddy sediments at ~40 m depth in central Long Island Sound, USA, during September 1988 (41°03.0'N, 72°53.1'W; station R, LISS-EPA Benthic Survey; and station DEEP of Aller, 1980). Bottom water temperature was 20°C. Sediment, collected by grab sampling from the upper ~25 cm, was immediately sieved with sea water through a 1.0 mm mesh to retain tubes. Only tubes containing living adult

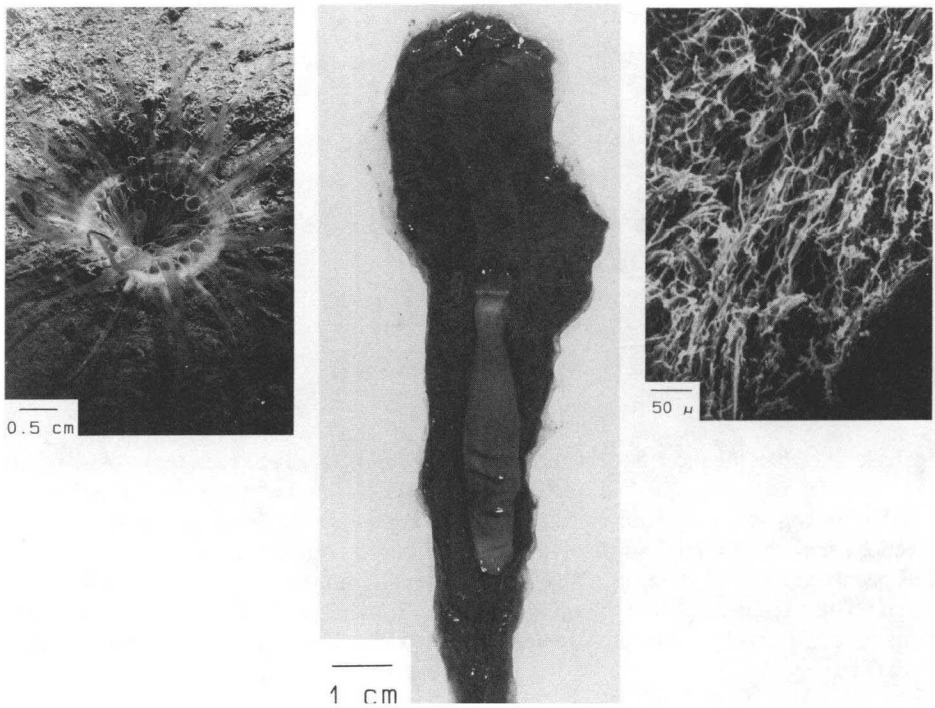

Figure 1. Left. *In situ* photograph of sediment surface from central Long Island Sound showing a specimen of *Ceriantheopsis americanus* expanding its tentacular crown from the tube opening (photo by W. Sacco). Middle. Intact tube removed from the sediment to show relation to size of the sea anemone. Right. SEM photograph of tube cross-section showing the concentric layering of fibers (freeze-dried).

specimens of *C. americanus* were used. After removal of the animals and subsequent gentle rinsing in sea water, tubes were kept at 2°C until initiation of experiments the following day. All tubes and tube sections were assumed to be identical for experimental purposes.

b. Experimental design

Decomposition characteristics of *C. americanus* tubes were studied in time series incubations for 122 days under 3 different experimental conditions. (1) exposed to oxic and (2) to anoxic sea water without sediment, and (3) buried in sealed containers filled with anoxic sediment. Before the start of experiments, representative tube samples were taken for determination of initial properties: loss-on-ignition (LOI), stepwise thermogravimetry (STG), particulate organic carbon (POC) and nitrogen (PON); bacterial counts; ATP concentration; and scanning electron microscopy (SEM). A conversion between wet weight (tubes blotted gently on filter paper for 15 sec) and dry weight (24 h at 80°C) was used to relate the start wet weights of tubes to start dry weights (dw/ww = 0.299 ± 0.025, N = 6; ±S.D.).

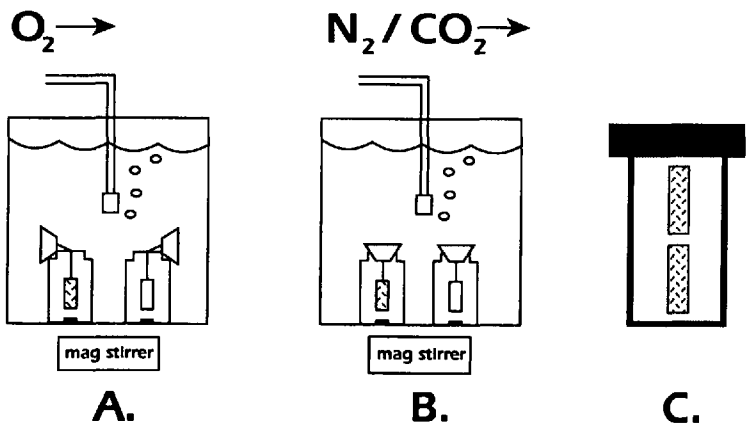

Figure 2. Sketch of the three basic incubation set-ups used. (A) Tube sections (cross-hatched) and control bags suspended in open bottles within an aerated reservoir (acronym: OXTUB). Silicon stoppers were closed briefly during solute flux measurements. (B) Tube sections and control bags suspended in closed anoxic bottles within an anoxic reservoir purged with N_2/CO_2 (acronym: ANTUB). In some cases bottles were opened briefly to allow metabolite exchange (ANTUB, op.). (C) Tube sections and control bags (not shown) embedded in anoxic sediment (stippled) enclosed in sealed centrifuge bottles (acronym: SEDTUB).

i. Experiment series 1. Oxic water without sediment (OXTUB). Sections of tubes weighing ~3 g wet wt. (ca. 1 g dry wt.) were separately enclosed in 7 × 4.5 cm Nytex 'tea' bags (65 μm mesh) and one bag placed in each of 10 continuously stirred 144-ml wide-mouth glass bottles. In order to keep the bags suspended freely in the water without any surface contact, threads woven through the mouth of each Nytex bag were inserted into silicone stoppers which were allowed to hang as a bag counter balance outside the mouths of the bottles (Fig. 2). Ten additional bottles containing empty Nytex bags acted as controls. All 20 OXTUB bottles were submerged in a 10-l polycarbonate jar containing filtered (0.4 μm) 29 ‰ sea water and placed in a dark incubator held at 20°C. The regularly renewed jar water was continuously aerated to ensure 100% oxygen saturation. Each bottle contained a Teflon-coated magnetic bar agitated by an underlying magnetic stirrer. Bottles were kept open to the aerated water except for brief periods when they were sealed with the silicone stoppers for solute exchange measurements (see below).

ii. Experiment series 2. Anoxic water without sediment (ANTUB). The basic set-up was similar to that used in the OXTUB experiment, however; in this experiment the continuously stirred bottles were initially filled with anoxic (N_2/CO_2 purged) sea water and kept permanently sealed with silicone stoppers (Fig. 2). Ten bottles contained tube sections enclosed in Nytex bags and 10 bottles acted as controls. The 10-l jar was continuously purged with a N_2/CO_2 mixture to maintain anoxic condi-

tions (pH = 8.1); which avoided any oxygen diffusion into bottles through the stoppers. The influence of metabolite build-up (such as sulfide) on microbial activity was also assessed by opening half of the bottles (indicated by the abbreviation 'op.' after the treatment acronym ANTUB) to the surrounding N_2/CO_2 flushed water in the jar for 30 min once a week, beginning at day 24. Water in the jar was periodically changed with fresh anoxic sea water.

iii. Experiment series 3. Anoxic sediment (SEDTUB). Sediment from ~10–20 cm depth collected at the same station as the tubes, was used to determine the decay rate of *C. americanus* tubes buried in anoxic sediment. The sediment was sieved by forcing it (no water added) through a 1.0 mm mesh sieve to remove any macrofauna present. Pieces of tubes weighing ~1.5 g wet wt. (0.5 g dry wt.) were each enclosed in 6 × 2.5 cm Nytex 'tea' bags and incubated in 10 sediment-filled, 50-ml polyethylene centrifuge bottles. In each case, two bags containing *C. americanus* tube sections were placed in succession down the middle of each centrifuge bottle and sediment alternately added and gently tapped to fill the remaining space (Fig. 2). Ten centrifuge bottles containing sediment and *empty* Nytex bags acted as controls. All centrifuge bottles were sealed with screwcaps, taped, placed in 2 liter polyethylene jars purged continuously with N_2/CO_2 (small valves allowed gas escape), and held within a dark incubator at 20°C throughout the experiment.

c. Sampling

i. Solute exchange. The exchange of oxidized and reduced inorganic solutes between *C. americanus* tubes and associated water in OXTUB and ANTUB experiments was determined at days 2, 8, 17, 24, 31, 53, 67, 107, and 122. The OXTUB bottles were examined for O_2, TCO_2 ($CO_2 + HCO_3^- + CO_3^{--}$), and DIN ($NH_4^+$, NO_2^- and NO_3^-) exchange. At each sample time, 4 bottles containing tubes (only 2 replicates at day 107 and 122) and 4 control bottles were randomly chosen and water samples taken before and after a 3–4 h incubation period during which bottles were closed with silicone stoppers. Water samples for O_2 and TCO_2 were analyzed immediately, whereas samples for DIN were filtered (0.4 μm), frozen and analyzed as soon as possible.

The ANTUB bottles were examined for TCO_2, SO_4^{--}, HS^- and NH_4^+ exchange. Samples were taken by syringe via a hypodermic needle inserted through the silicone stoppers of 4 randomly chosen bottles containing tubes (due to the separation of bottles into closed 'cl.' and opened 'op.' treatments only 3 (day 31), 2 (day 53 and 67), and 1 (day 107 and 122) replicates were available for flux measurements) and 4 control bottles. The volume of water removed was simultaneously replaced with ambient anoxic water from the ANTUB jar which entered through a second hypodermic needle. About 10% of the bottle volume was removed per sample. All mass balance calculations are corrected for this dilution based on measured solute

concentrations in the replacement water. Samples for TCO_2 were analyzed immediately; filtered (0.4 μm) samples for SO_4^{--} were acidified with 50 μl 12 M HCl and stored at 2°C until analysis; samples for HS^- received 0.5 ml of 0.05 M ZnAc to precipitate ZnS and were stored at 2°C until analysis; and samples for NH_4^+ were stored frozen and analyzed as soon as possible.

ii. Tubes, sediment and pore water. Samples of tube material and sediment from all 3 experimental series were taken for particulate and pore water analysis at days: 8, 17, 30, 68 and 122. At each sampling date 2 bottles from the OXTUB and the ANTUB experiment, and 2 centrifuge tubes with *C. americanus* tubes from the SEDTUB experiment were used. A corresponding number of controls containing empty Nytex bags were sampled at the same time. The OXTUB and ANTUB tubes were removed from the Nytex bags, gently blotted on filter paper for 15 sec., and weighed (wet wt.). The tubes were divided into 5 similar transverse sections for the following treatments: 1. dried at 80°C for dry weight, LOI, STG, POC and PON determinations; 2. frozen; 3. preserved in 2% formaldehyde for SEM examination; 4. preserved in 3% NaCl solution with 0.3% EM grade glutaraldehyde for direct bacterial counts and SEM examination; 5. extracted immediately in boiling phosphate-citrate buffer for total ATP determination.

The SEDTUB containers were centrifuged at 2000 rpm for 10 minutes to retrieve pore water for TCO_2, SO_4^{--}, HS^- and NH_4^+ analysis. Water samples were treated in the same way as those from the ANTUB experiment. Subsequently, the *C. americanus* tubes (in Nytex bags) were removed from the sediment, gently rinsed in sea water, blotted on filter paper for 15 sec. and weighed. A similar sectioning and treatment as mentioned above for OXTUB and ANTUB tubes was performed. Sediment from the SEDTUB experiment was treated as the tubes, except that no sample was preserved in formaldehyde.

d. Analysis

i. Water samples. TCO_2 was analyzed in triplicate by a modified version of the diffusion cell technique of Willason and Johnson (1986). Samples (50 μl) were injected into a stream of 10 mM HCl. This sample/carrier stream was directed into a diffusion cell composed of two Plexiglas halves each containing a 230 mm long; 3.2 mm wide; and 0.127 mm deep groove. A piece of non-laminated Gore-Tex (W. L. Gore Co.) hydrophobic teflon membrane (pore size 0.02 μm) was used to separate the two halves. Gaseous CO_2 from the sample/carrier stream on one side of the cell diffused across the membrane into an acceptor/indicator stream composed of 2.8 mM $NaHCO_3$, 2.2 mM Na_2CO_3 on the other side. The change in total ion strength of the acceptor/indicator stream caused by CO_2 diffusing from the sample/carrier stream was detected on a Dionex Conductivity Detector. A standard curve allowed

calculation of TCO_2. Precision was usually better than 1% (this method has since been modified for increased sensitivity, Hall and Aller, 1991).

Oxygen was analyzed by the standard Winkler technique directly in the 10-ml collection syringes used during sampling. Ammonium was analyzed by the phenol-hypochlorite indophenol blue method of Solorzano (1969). Nitrite and nitrate were determined on an autoanalyzer by a modified Cd-Cu reduction-ethylenediamine dichloride method (Strickland and Parsons, 1972). Sulfate was determined gravimetrically after $BaSO_4$ precipitation. Free HS^- was analyzed by the diamine method of Cline (1969).

ii. Solid phase. The 80°C pre-dried tube and sediment samples were further dried at 130°C for 6 h to remove adsorbed water (typically 2–3%). Subsequently, the STG (stepwise thermogravimetric) procedure of Kristensen (1990) was performed on subsamples to help determine the composition of the tubes. Briefly, the 130°C dried samples were combusted at 280°C for 6 h, cooled in a desiccator and weighed. The same samples were then combusted at 520°C for 6 h, cooled in a desiccator and weighed. The weight loss in the range 280–520°C (PII) was related to the total loss on ignition (LOI) in the range 130–520°C (PI + PII) to obtain the Rp index, as follows: Rp = PII/(PI + PII). Low Rp's (around 0.2) are typical for materials rich in aliphatic compounds (lipids, carbohydrates), whereas high Rp's (0.5–0.6) represent aromatic compounds and materials rich in nitrogen (humates, proteins). Precision was usually better than 5%.

Particulate organic carbon (POC) and nitrogen (PON) of 130°C pre-dried subsamples were analysed on a Hewlett-Packard 185B CHN-analyzer. Inorganic carbon content was determined from the POC content of 520°C combusted samples (Kristensen and Andersen, 1987).

The linear NH_4^+ adsorption coefficient, K^*, of freshly collected *C. americanus* tube material was estimated by exposure of tube material to sea water containing varying concentrations of NH_4^+ (0.1, 0.3, 0.5, 0.7, 1.0 mM). By measuring the uptake and release of NH_4^+ at 1 h intervals over a 6 h period (stable after 3–4 h) the adsorption coefficient was determined as the slope (at 6 h) of adsorbed (y) versus soluble NH_4^+ (x) concentrations. A dimensionless form of the coefficient K, was calculated using the mass/volume ratios of tube/water in each experimental series.

Bacterial abundances of tubes, sediment and water samples were enumerated by the direct count epifluorescence method of Hobbie *et al.* (1977) as modified by Watson *et al.* (1977). Tube samples were prepared for both bacterial counts and ATP extractions by grinding known weights of wet tube material along with sterile glass beads in a micro-tissue grinder. Sediment and tube adenosine triphosphate (ATP) concentrations were extracted in duplicate using a phosphate-citrate buffer (Bulleid, 1978). Extracts were assayed for ATP using the firefly bioluminescent procedure

(Holm-Hansen and Booth, 1966). ATP concentrations were calculated using a series of standard ATP recovery curves determined with ATP-free sediment from the same collection area. These curves allow correction for extraction efficiency and chemical interference as a function of extracted sediment weight (J. Aller, unpublished).

3. Results

a. Solid phase

The fibrous ca. 1 mm thick inner lining typical of inhabited *Ceriantheopsis americanus* tubes was always embedded in a more porous 2–3 mm thick outer layer. The inner lining was neatly woven from silk-like fibers, whereas the outer layer consisted of a fibrous matrix rich with occluded silt and clay particles (Fig. 1). Under SEM there were no discernible morphological changes in fibers during the experiment. The inorganic sediment particles in the outer tube layer contributed to an overall low organic content of tubes. Ignition loss, organic carbon and nitrogen content of tubes used in the experiments were 14.5 ± 4.0, 4.9 ± 1.7, and 1.10 ± 0.44% (±S.D., $N = 3$), respectively, only 2–5 times higher than the surrounding sediment (6.7 ± 0.2, 1.8 ± 0.1, and 0.22 ± 0.02%, respectively). Oxic OXTUB tubes appeared brown probably due to the presence of oxidized Fe compounds, whereas the anoxic ANTUB and SEDTUB tubes were black from the presence of FeS.

All tubes changed considerably in weight during the decomposition experiments (Fig. 3A). The unexpected, but consistent, weight increase observed initially from day 0 to 8 was probably caused by systematic weighing errors. The dry weight of tubes was determined indirectly from wet weight measurements after manual blotting on filterpaper using a dw/ww conversion factor obtained from dried subsamples. Such a procedure has a high degree of uncertainty, because it depends on exactly the same handling at every sampling date. Although no precise quantitative information can be inferred from the dry weight data, the temporal weight pattern suggested an exponential loss after day 8 with more than half of the total weight loss occurring by day 30.

Both the molar C:N ratio (Fig. 3B) and Rp index (Fig. 3C) of the tube material were affected dramatically during the first 30 days, with only minor subsequent changes. This general pattern appeared independent of the actual treatment. The low tube C:N ratio (5.0–5.5, day 0) showed a rapid initial decrease to minimum values of 4.3–4.7 at day 17. OXTUB and SEDTUB remained constant thereafter, whereas in ANTUB tubes C:N increased gradually to a final value of 5.1.

The Rp index was lowest for SEDTUB (0.49) and highest for OXTUB (0.54) and ANTUB (0.55) initially (Fig. 3C). After a decrease during the first days, minimum values of 0.47, 0.52 and 0.50 were found at day 17, 30 and 8, respectively. Subsequently, Rp increased and gradually reached maximum values of 0.54–0.57 at the end. The changes in Rp were least dramatic in OXTUB tubes.

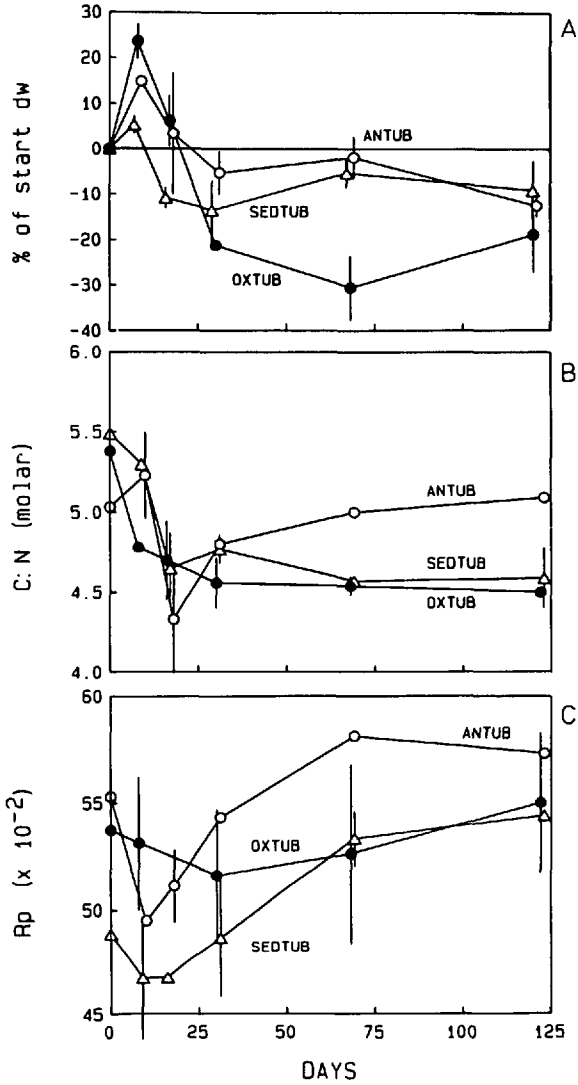

Figure 3. Solid phase parameters during a 122 day decomposition period of *C. americanus* tubes suspended in oxic sea water (OXTUB, ●), free in anoxic sea water (ANTUB, ○), and buried in sediment (SEDTUB, △). (A) dry weight; (B) molar C:N ratio; (C) Rp index from STG analysis. Error bars represent: (A) ± S.E. (N = 4); (B) and (C) range of 2 measurements (except for ANTUB after day 30 where only one sample is analyzed per date).

b. Solute exchange

i. OXTUB. After a few days lag period, CO_2 production and DIN exchange were evident in all 3 experiments. In the OXTUB experiment, CO_2 production increased rapidly from an initial low rate, 0.2 umol g dw^{-1} h^{-1}, to a peak of 1.9 μmol g dw^{-1} h^{-1} (Fig. 4A) at day 24. Subsequently, the rate decreased until a slight CO_2 uptake was

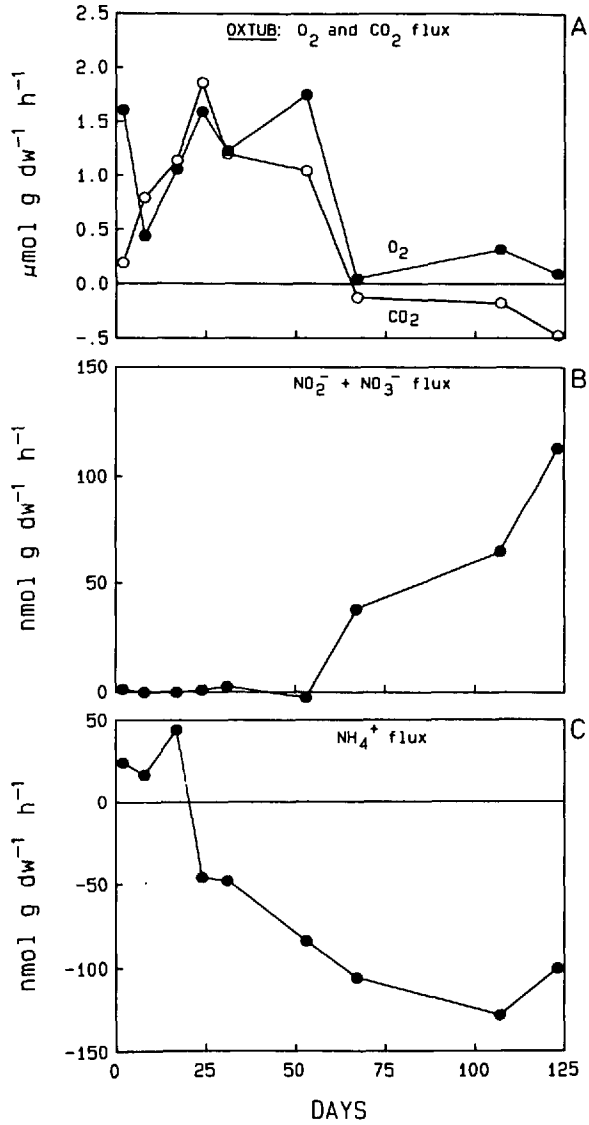

Figure 4. Weight-specific exchange rates of inorganic solutes in *C. americanus* tubes suspended in oxic sea water during a 122 day decomposition period. (A) O_2 (●) and TCO_2 (○); (B) NO_2^- + NO_3^-; and (C) NH_4^+. Negative values indicate net consumption.

observed at day 67 and thereafter. The precision of both O_2 and CO_2 flux was typically S.D. = 10–30% of the mean (N = 4) during the first 53 days. The rate of O_2 consumption generally followed CO_2 production, except at the initial sampling date. The initial rate of O_2 consumption was very high (1.6 μmol g dw^{-1} h^{-1}); probably due to oxidation of sulfides or reduced Fe. The observed excess O_2 uptake relative to CO_2 exchange after day 31 correlated with the initiation of NO_2^- + NO_3^- production. Net

NO_2^- + NO_3^- production, that started after day 53, showed a continued increase throughout the experiment reaching 113 nmol g dw^{-1} h^{-1} at day 122. A considerable nitrogen removal, presumably by denitrification, was evident from the high uptake of NH_4^+ after day 17. Ammonium uptake was always higher than or equal to net NO_2^- + NO_3^- production, although NH_4^+ production must have occurred from mineralization processes in the tubes. Net ammonium production was only evident as a low release rate of 16–44 ± 5–15 nmol g dw^{-1} h^{-1} during the first 17 days (N = 4).

ii. ANTUB. Significant rates of solute exchange showing a time dependent decrease were observed in ANTUB bottles both with and without tubes (Fig. 5). The exchange rates of CO_2, SO_4^{--}, and HS^- in the presence of tubes were stimulated 5 times compared to controls during the first 30 days of anoxia (average tube rates i.e. tube − control, for exchange of CO_2, SO_4^{--}, and HS^- were 512, −488, and 238 nmol g dw^{-1} h^{-1}, respectively) and only about 2 times thereafter (59, −8, and 4 nmol g dw^{-1} h^{-1}, respectively). The microbial activity in the controls may reflect dissolved organic substrates in the sea water and degradation of the polyester/cotton thread needlework of the Nytex bags. The high metabolic activity observed initially in ANTUB tube bottles was not coupled to a net NH_4^+ production. Release of NH_4^+ in control bottles was insignificant. Ammonium adsorption by tubes was low (K^* = 0.46 ml g dw^{-1}), about half of Long Island Sound bulk sediments. The dimensionless adsorption coefficient in bottles (K ~ 0.03) is therefore sufficiently small that adsorption was not a major consideration given the solid/fluid ratios in the experiments. The relationship between CO_2 and both SO_4^{--} and HS^-, a linear slope around 0.5, indicates that sulfate reduction was the predominant respiration process occurring during anoxic tube decomposition (Fig. 6A,B). The 122 d integrated production of CO_2 and HS^- by tubes in the periodically opened (op.) bottles was 2 times higher than in the permanently closed (cl.) bottles (Table 1). Sulfide concentrations in op. bottles were low (max 500 μM) compared to cl. bottles (> 1.5 mM after day 30). NH_4^+ production was higher by a factor of 1.3 in op. bottles. After the initial 20 day lag phase in NH_4^+ production, the C:N flux ratio in cl. bottles approached 20 throughout the experiment (Fig. 6C); indicating mineralization of carbon rich compounds.

iii. SEDTUB. The impact of tubes on solute consumption/production patterns in the SEDTUB series was masked by the background microbial activity in the sediment. However, reaction rates were always significantly higher in sediment with tubes than in those without tubes (Fig. 7). Rates within tubes were 30–50 times higher than sediment rates on weight basis. Sediment properties and reaction rates of all dissolved species examined were similar to those previously reported at 10 cm depth in Long Island sediments by Martens *et al.* (1978); Aller (1980); and Aller and Yingst (1980). About half of the excess CO_2 production caused by tubes (average tube rate:

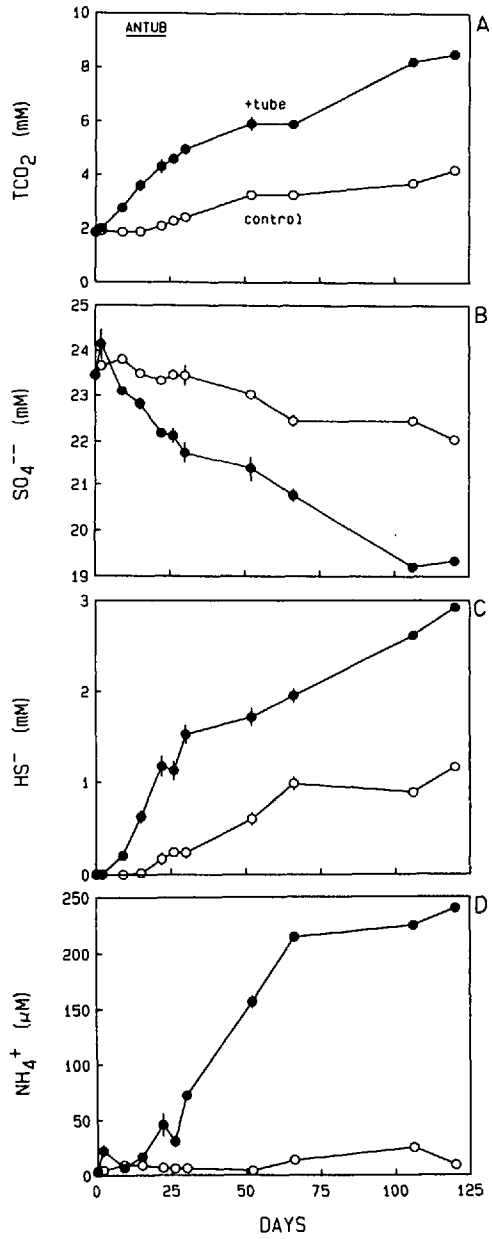

Figure 5. Concentrations of inorganic solutes in closed anoxic bottles containing *C. americanus* tubes suspended in sea water (+tube, ●) and control bottles without tubes (control, ○) during a 122 day decomposition period. (A) TCO_2; (B) SO_4^{--}; (C) HS^-; and (D) NH_4^+. Error bars represent S.D.

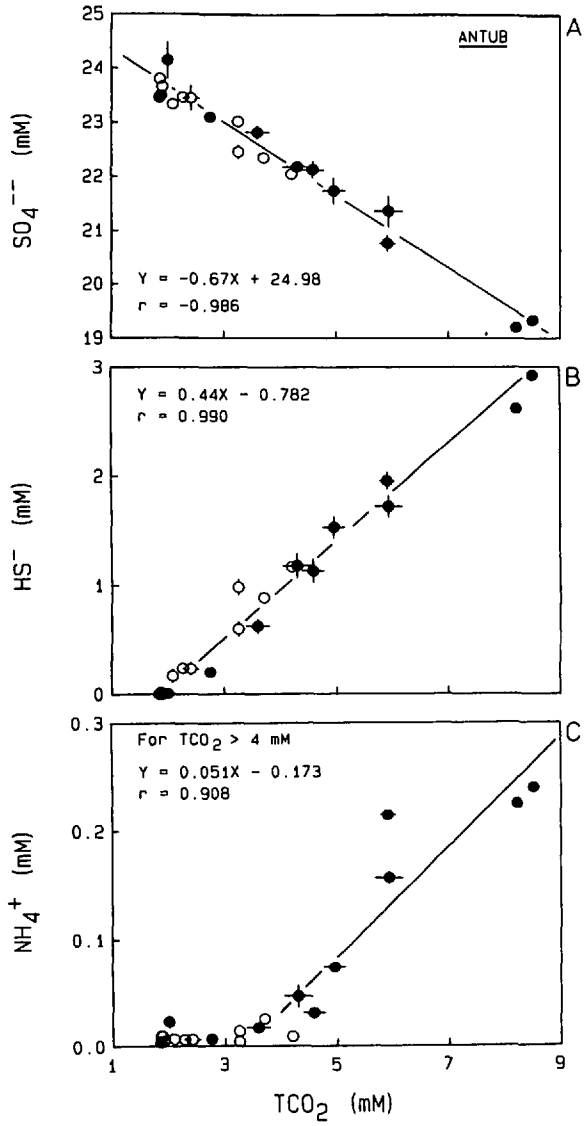

Figure 6. The relationship between concentrations of TCO_2 and (A) SO_4^{--}; (B) HS^-; and (C) NH_4^+ in anoxic bottles with (●) and without (○) *C. americanus* tubes. The equations obtained by least squares regression analysis are given. Error bars represent S.D.

337 nmol g dw^{-1} h^{-1}) occurred within the first two weeks (Fig. 7A). Only limited stimulation of SO_4^{--}, HS^-, and NH_4^+ reaction rates occurred in this period. The stimulation of SO_4^{--} reduction and HS^- production (from day 8) in the presence of tubes (average tube rates: −75 and 16 nmol g dw^{-1} h^{-1}) appeared constant through-

Table 1. Integrated weight-specific exchange of inorganic solutes by *C.americanus* tubes in the various treatments (OXTUB, ANTUB, SEDTUB) and sediment (SED) in the SEDTUB experiment during the 122 day experimental period, given as μmol g dw^{-1}. The abbreviations cl. and op. denote permanently sealed bottles and bottles that were opened once a week, respectively.

Treatment	ΣJ_{O_2}	ΣJ_{CO_2}	$\Sigma J_{SO_4^{--}}$	ΣJ_{HS^-}	$\Sigma J_{NH_4^+}$	ΣJ_{DIN}
OXTUB	2253	1563	—	—	−227	−146
ANTUB:						
cl.	—	696	−420	267	35	35
op.	—	1154	—	561	47	47
SEDTUB	—	277	−245	36	32	32
SED	—	8.5	−4.8	0.08	0.68	0.68

out the experiment (Fig. 7B,C). The CO_2/SO_4^{--} relationship in Figure 8A (slope −0.63) indicates that sulfate reduction was the dominant anaerobic respiration process occurring in sediment both with and without added tubes. The net HS^- production found in tube sediment compared to the control (Fig. 7C) was obscured by precipitation reactions. Accordingly, no clear CO_2/HS^- relationship was evident in this experiment (Fig. 8B). Nearly all excess NH_4^+ in the tube sediment was produced between day 17 and day 30 (average tube rate: 34 nmol g dw^{-1} h^{-1}), just after the peak in CO_2 production (Fig. 7D). Both the tube sediment and the control sediment exhibited a C:N flux ratio around 20 (Fig. 8C); whereas, by difference, an estimate of 12 was evident for tubes.

The integrated tube CO_2 production (viz. microbial activity) over the entire experimental period followed the sequence: OXTUB > ANTUB > SEDTUB (Table 1). The observed flux ratios of 5.6:2.5 (op. 4.2):1 indicate that free sulfide or other metabolites in sediment pore waters may inhibit microbial activity. OXTUB and occasionally opened ANTUB (op.) bottles both have rates significantly higher than permanently closed sulfide rich ANTUB (cl.) bottles. In the SEDTUB experiment other causes than free sulfide must be responsible for the low rate of decomposition.

c. Bacteria and ATP

The density of bacteria and ATP concentration in *C. americanus* tubes, 10^9–10^{10} g dw^{-1} and 3–60 ng g dw^{-1}, respectively, peaked within the first 30 days in all three experiments. The range within duplicates was typically less than 40% of the mean. Both parameters followed largely the same temporal pattern as metabolic CO_2 production (Figs. 9, 10, 11). An exception from this was an initial decrease in bacterial numbers in ANTUB tubes (Fig. 10C). However, the abundance of bacteria and ATP, as well as CO_2 flux, was stimulated in ANTUB op. bottles that had been opened regularly compared to the permanently closed (cl.) bottles. In OXTUB tubes, bacteria, ATP, O_2 flux, and CO_2 flux showed almost identical patterns,

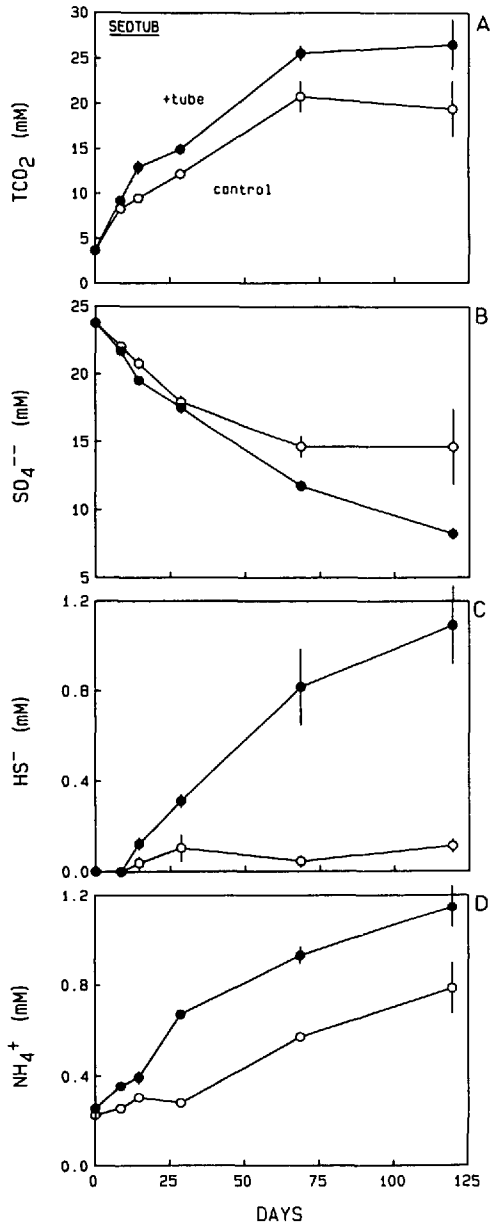

Figure 7. Pore water concentrations of inorganic solutes in Long Island Sound sediment containing *C. americanus* tubes (+tube, ●) and control sediment without tubes (control, ○) during a 122 day decomposition period. (A) TCO_2; (B) SO_4^{--}; (C) HS^-; and (D) NH_4^+. Error bars represent S.D.

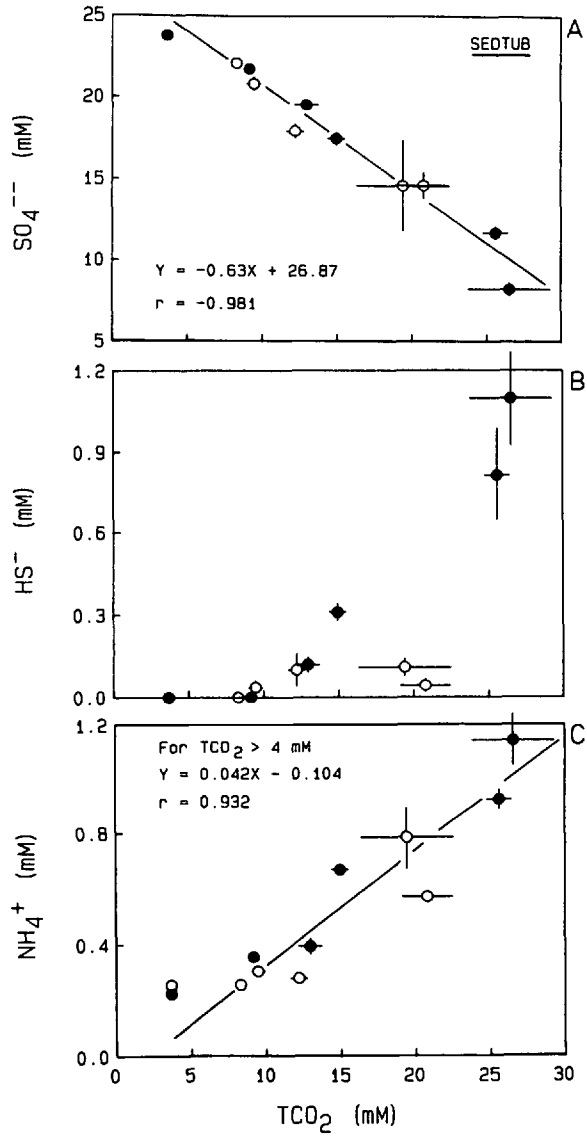

Figure 8. The relationship between pore water concentrations of TCO_2 and (A) SO_4^{--}; (B) HS^-; and (C) NH_4^+ in Long Island Sound sediment with (●) and without (○) embedded *C. americanus* tubes. The equations obtained by least squares regression analysis are given. Error bars represent S.D.

indicating a close relationship between these parameters (Figs. 4A, 9). Regression coefficients ranged from 0.718 to 0.978. A similar, but less pronounced, pattern was found in the SEDTUB experimental tubes and sediment (Fig. 11). The ATP values in the sediment, reflecting microorganisms as no living meiofauna were found, were

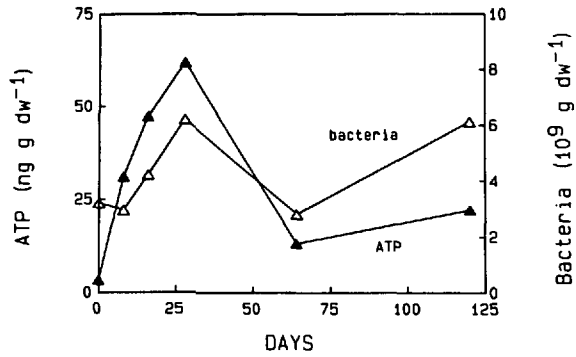

Figure 9. Weight-specific changes in ATP concentrations (▲) and bacterial numbers (△) from *C. americanus* tubes kept free in oxic sea water for 122 days.

one order of magnitude lower than in tubes; whereas bacterial numbers were 2–3 times higher. On average, both parameters were almost two times higher in sediment with tubes than without (Table 2). Handling (i.e. mixing and sieving), however, may be responsible for the unexpected initial peak in bacterial numbers in SEDTUB sediment without tubes.

An inter-treatment comparison reveals a close relationship between bacterial numbers and ATP content in both tubes and sediment (Table 2). No apparent difference in the average bacteria and ATP values occurred between ANTUB and SEDTUB tubes. OXTUB tubes, on the other hand, had values 2–4 times higher than in the other treatments (highest for ATP). The bacterial cell and POC specific ATP concentrations clearly substantiate the general activity sequence: OXTUB > ANTUB ≥ SEDTUB ≫ SED+ ≥ SED− (Table 3) (where SEDTUB is the tube proper and SED+ refers to the *sediment* in centrifuge bottles containing tubes and SED− refers to *sediment* in control bottles without *C. americanus* tubes). The very low sediment activity as indicated by the ATP concentration was not reflected in the POC specific bacterial density, sediment counts being an order of magnitude higher than tube counts.

d. Decay rate

Degradation of *C. americanus* tubes was assumed to follow a simple exponential ('one-G') first-order type of reaction: $G_t = G_o e^{-kt}$. The use of a composite exponential ('multi-G') model (Berner, 1980; Westrich and Berner, 1984) or a "decaying coefficient" model with an exponentially decreasing decay constant (Godshalk and Wetzel, 1978; Moran *et al.*, 1989) may describe decomposition processes more precisely than a 'one-G' model. However, the nature of our data justified the use only of the latter model.

Decay constants (k) for dw were estimated from the observed weight loss of tubes ($G_o - G_t$) during the experiment (ignoring the erroneous weight gain measured at

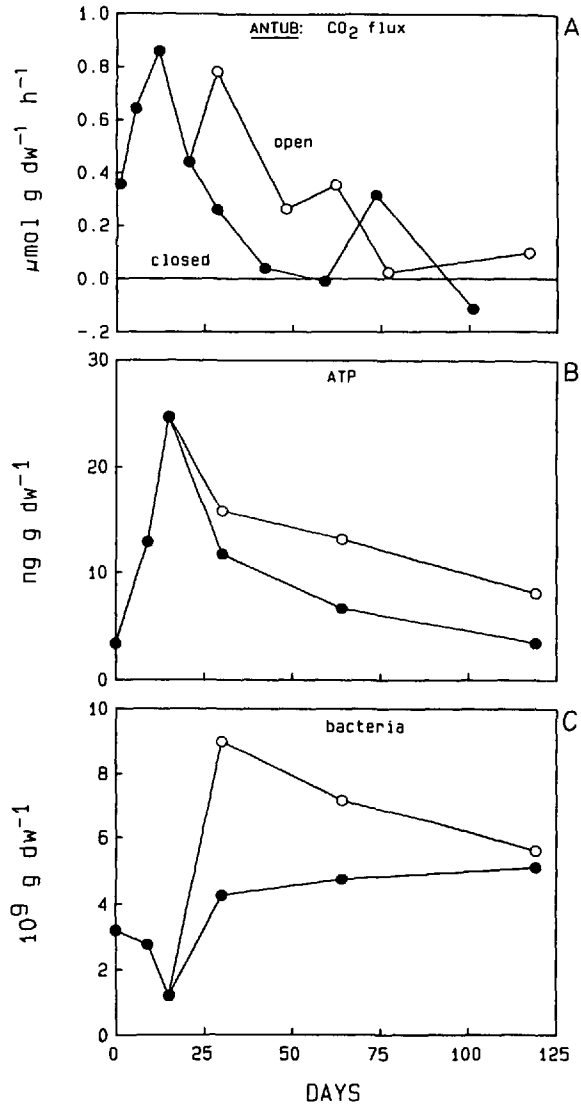

Figure 10. (A) Weight-specific TCO_2 exchange, (B) ATP concentrations and (C) bacterial numbers in *C. americanus* tubes kept free in anoxic sea water for 122 days. Closed symbols represent permanently sealed (cl.) bottles and open symbols represent bottles that were opened (op.) once a week.

day 8). Cumulative solute fluxes related to the initial solid phase content were used in the k estimate for carbon and nitrogen (assuming a C:N ratio of 20 in the OXTUB losses). The decay constants, estimated for the entire 122 d experimental period, appeared relatively low (Table 4). Values of k for dw and POC were almost identical in all experiments, providing half-lives of 0.9–1.1, 1.7, and 2.4–3.1 yr for OXTUB,

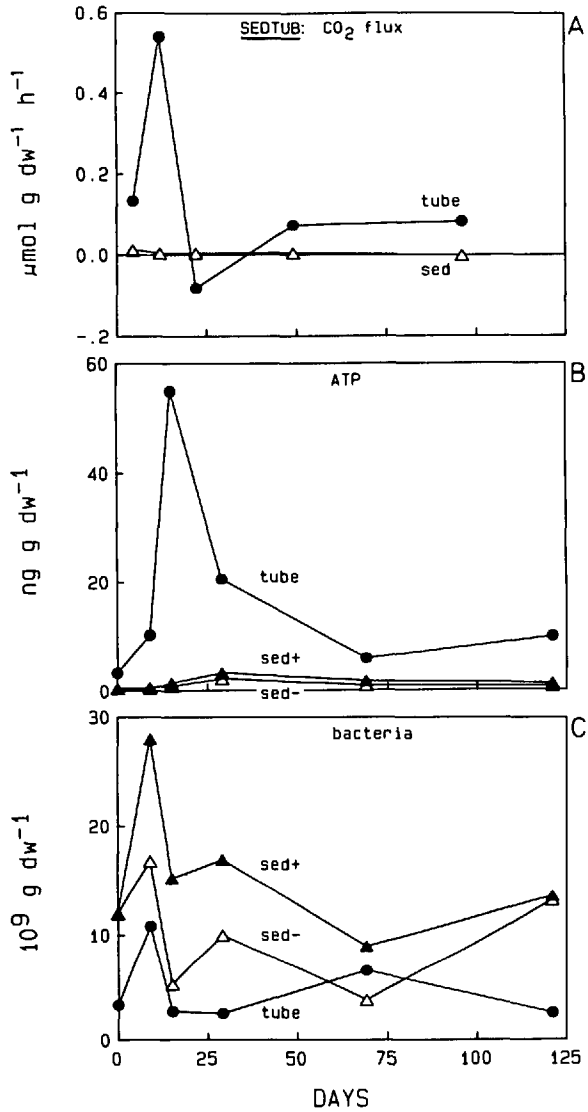

Figure 11. (A) Weight-specific TCO_2 exchange, (B) ATP concentrations and (C) bacterial numbers in *C. americanus* tubes kept buried in anoxic Long Island Sound sediment for 122 days (●). Data for the sediment with (SED+, ▲) and without (SED−, △) embedded tubes are presented.

ANTUB and SEDTUB tubes, respectively. The similarity in these two estimates is surprising because only 5% of the dw is POC. A part of the loss in dw is probably caused by a gradual release of occluded inorganic sediment particles *in proportion* to organic matter decay. In both OXTUB and ANTUB bottles, particles < 65 μm dropped from the Nytex bags to the bottom throughout the experiments. The decay

Table 2. Ratios between pairs of the various *C.americanus* tube treatments and sediments (SED+, with and SED−, without embedded tubes) of bacterial count (R_{bact}) and ATP concentration (R_{ATP}). Values are mean of ratios for the entire experimental period ± S.D. ($N = 6$).

Pairs	R_{bact}	R_{ATP}
OXTUB/ANTUB	1.6 ± 1.1	3.6 ± 2.1
OXTUB/SEDTUB	1.8 ± 1.0	2.3 ± 0.9
ANTUB/SEDTUB	1.1 ± 0.8	0.8 ± 0.4
SED+/SED−	2.0 ± 0.8	1.7 ± 0.2

constants for PON were generally 2–4 times lower than for dw and POC, indicating a preferential decomposition of carbon. The very low decay rate of organic matter in the SEDTUB sediment, with half-lives for POC and PON of 39 and 53 yr, respectively, reflected the sampling depth, age and chemical composition of the sediment detritus.

4. Discussion

Burrowing cerianthid sea anemones generally line their burrows with a tube of interwoven threads ~2 mm long and 2–5 μm wide, formed from thousands of discharged special nematocysts: ptychocysts (Mariscal *et al.,* 1977). The stickiness and interwoven properties of the long ptychocyst threads form an extremely tough and resilient tube and promote incorporation of sediment into the outer matrix. In fact, 85% of the tube dry weight is typically composed of inorganic sediment particles. The radially layered construction suggests that ptychocysts are continuously added to the inside of the tube during the life span of the animal. In this study, an average sized individual of *C. americanus* weighing 0.9 g wet wt maintained a 1.04 g dw tube with 65 mg POC g^{-1} and 15 mg PON g^{-1}. If tube construction rate balances growth and decay, tube/body weight ratios should remain approximately constant.

Table 3. ATP content per bacterial cell, ATP content per g organic carbon (POC), and number of bacteria per g organic carbon (POC) of *C.americanus* tubes in the various treatments (OXTUB, ANTUB, SEDTUB). Results from sediment with (SED+) and without (SED−) embedded tubes are listed for comparison. Values are mean of ratios for the entire experimental period ± S.D. ($N = 6$).

Treatment	ATP/bact. (10^{-9} ng/cell)	ATP/POC (ng/g)	bact./POC (10^{10} cells/g)
OXTUB	8.00 ± 3.18	458 ± 234	6.2 ± 2.3
ANTUB	3.99 ± 1.29	186 ± 76	6.9 ± 3.7
SEDTUB	3.12 ± 2.98	183 ± 117	9.1 ± 6.9
SED+	0.11 ± 0.07	75 ± 52	83.6 ± 30.7
SED−	0.13 ± 0.09	52 ± 32	54.1 ± 24.5

Table 4. Total loss of *C.americanus* tube dry material (dw, $G_o - G_t$), organic carbon (POC, total flux, ΣJ_C), and organic nitrogen (PON, total flux, ΣJ_N) in the various treatments (OXTUB, ANTUB, SEDTUB) during the experimental period (t = 122 d). Results from the sediment (SED) used in the SEDTUB experiment are included. Data are given as % of initial content. The decay constant (k, yr^{-1}) is estimated according to: $G_t = G_o e^{-kt}$.

	dw		POC		PON	
Treatment	$G_o - G_t$	k	ΣJ_C	k	ΣJ_N	k
OXTUB	18.9	0.637	22.1	0.759	6.31	0.198
ANTUB	12.6	0.409	12.6	0.409	3.23	0.100
SEDTUB	9.2	0.292	7.0	0.221	3.21	0.099
SED	—	—	0.58	0.018	0.44	0.013

Oxic and anoxic microbial decay of freshly collected *Ceriantheopsis americanus* tubes are generally 1–2 orders of magnitude slower than reported for most fresh plant materials such as planktonic debris (e.g. Jewell and McCarty, 1971; Hargrave and Phillips, 1989) and aquatic macrophytes (e.g. Godshalk and Wetzel, 1978; Rice and Tenore, 1981; Andersen and Hargrave, 1984; Twilley *et al.*, 1986). In contrast, the observed low C:N ratio and high Rp index of the tubes (Fig. 3B,C) are typical for proteinaceous materials and often imply a potential for rapid decomposition. The relatively refractory nature of *C. americanus* tubes must be a function of the chemical structure. Bishop *et al.* (1978) found that more than 95% of the organic pool in *C. americanus* tubes consists of a fibrous protein polymer termed cerianthin. The remaining 5% of the organic pool is mainly nitrogen poor non-structural carbohydrates. The chemical resemblance of ptychocyst threads to decay resistant silk fibroin is striking, although the amino acid composition is slightly different. Glycine accounts for 40–45% of the total amino acid content in both compounds, whereas proline and alanine are responsible for 14 and 4% in cerianthin versus about 0.5 and 28% in commercial silk fibroin (Lucas and Rudall, 1968; Fraser and MacRae, 1973; Bishop *et al.*, 1978). The low NH_4^+ adsorption capacity, which indicate that there must be relatively few exposed functional groups capable of binding NH_4^+, is consistent with a dominance of amino acids with small side chains (e.g. glycine). The content of condensed or aromatic polymers with few exposed side chains is generally an important factor controlling the decay of organic matter (Hodson *et al.*, 1983; Henrichs and Doyle, 1986; Moran *et al.*, 1989). During microbial degradation of biopolymers, easily-attacked side chains are removed prior to cleavage of resistant intermonomeric linkages (Benner *et al.*, 1984; Wilson, 1985).

The metabolic activity in all experimental treatments followed the classic temporal pattern. There was a steep increase from a low level initially to a peak after a few days, followed by rapidly (exponential) decreasing activity (Figs. 4A, 10A, 11A). The characteristic decrease in C:N and Rp observed initially during both oxic and anoxic tube decay (Fig. 3B,C) is probably caused by relative loss of the small carbohydrate

pool and exposed side groups of the tube cerianthin. Preferential decomposition of the carbohydrate pool results in a decreasing C:N ratio. The decline in Rp values, which coincides with the initial increase during early decomposition in both ATP and bacteria (Figs. 4A, 10A, 11A), indicates that simultaneous production of labile material of less condensed structure also occurs, presumably bacterial tissue and excreted (nitrogen rich) mucopolysaccharides (Hobbie and Lee, 1980). Incorporation of nitrogen by bacteria during the initial growth phase is probably responsible for the lack of any significant net production of remineralized nitrogen in the form of NH_4^+ and NO_2^- +NO_3^- during the first 20–25 days (Figs. 4, 5, 7). The subsequent steady C:N ratio and increasing Rp index, when both ATP and bacteria are declining, suggests that decay of organic matter associated with dead bacteria occurs when no further labile tube-compounds are available (Novitsky, 1986). The more refractory cerianthin and possibly bacterial cell remains (Nelson *et al.,* 1979; Blackburn, 1988) are left as substrate for further very slow decay. The decline in both bacterial activity and growth from around day 25, coinciding with a significant net production of remineralized inorganic nitrogen (DIN) (Figs. 4, 5, 7), demonstrates that the availability of labile carbon is the limiting factor during the late stage of decomposition. The C:N ratio in the residual tube material remains relatively low, indicating that nitrogen can be incorporated and preserved in refractory compounds via at least two totally different pathways in the bioturbated zone of marine sediments. One path is the *direct* production of refractory biopolymers such as tube material, and the second is the traditionally recognized binding of nitrogen into humic geopolymers (Rice, 1982).

Aerobic microbial processes (OXTUB) are at least twice as rapid as anaerobic (ANTUB) in net tube decay (Table 1, 4). The indication of an overall lower metabolic activity under anoxic conditions, as observed in the flux measurements, is confirmed by the 2–3 times lower ATP/bacteria and ATP/POC ratios in anoxic than in oxic tubes (Table 3). No significant difference in bacterial numbers are evident between the two experimental treatments. Interpretation of results from oxic decomposition experiments, however, are complicated by the presence of chemoautotrophic microbial processes; i.e. nitrification and sulfide oxidation. These processes consume both O_2 and CO_2 during organic matter production, and partially negate the use of net fluxes as a basis for decay estimates. The apparent CO_2 consumption after day 53, i.e. lower production in the OXTUB tube bottles than in the randomly chosen controls, is probably due to assimilation by nitrifying bacteria in the tubes. This is supported by the exchange pattern of O_2, NO_2^- + NO_3^-, and NH_4^+ (Fig. 4A-C).

Degradation of structural biopolymers, such as lignins and aromatic hydrocarbons, is generally known to be hampered by lack of molecular oxygen (Crawford *et al.,* 1977; Fenchel and Blackburn, 1979; Henrichs and Reeburgh, 1987). Low efficacy of hydrolytic and fermentative processes in the primary enzymatic attack on chemically

complex biopolymers may be the rate limiting step in anaerobic tube decay. These reactions supply substrates (e.g. fatty acids) for sulfate reduction, which is the dominant terminal respiration process. The absence of oxygen, however, is not the only major factor influencing decomposition rates in anoxic environments, as many compounds are readily degraded under anaerobic conditions (Foree and McCarty, 1970; Westrich and Berner, 1984; Henrichs and Reeburgh, 1987; Kristensen and Blackburn, 1987). The presence of high concentrations of metabolites, e.g. sulfide, may inhibit anaerobic decomposition processes (Jørgensen, 1983). This effect is evident from the present experiments where microbial activity (both fluxes, ATP and bacteria) in anoxic (ANTUB) tubes almost doubled when the bottles were opened frequently to remove free sulfide and associated metabolites (Fig. 10).

In situ decomposition of *C. americanus* tubes is, except for the uppermost protruding few centimeters, expected to occur almost entirely under anoxic conditions. Even during the inhabitants normal activity cycles, hardly any oxygen is transported into the tubes. Sassaman and Mangum (1974) found that O_2 concentration in the nonventilated tubes of *C. americanus* was always below 30% of air saturation. Oxygen needed by the animal for respiratory purposes is supplied by diffusion into the gastrovascular fluid through the relatively thin walled crown. Only limited amounts of O_2 are likely to diffuse back through the thick body wall into the tube shaft. The outer margin of the tubes are also in continuous and intimate contact with the bulk anoxic sediment. Decay rates obtained from tubes buried in sediment are therefore expected to mimic the natural conditions more closely than rates obtained from tubes free in water.

Burial in anoxic sediment reduces tube degradation significantly. Decay rates of tubes embedded in Long Island Sound sediment are about half of that when tubes are suspended in anoxic sulfidic water, while both bacterial numbers and ATP content appear unaffected (Table 2). The cause for such inhibition, even when the free sulfide level in the pore water is low, may be the cumulative inhibitory action of metabolites combined with slower diffusion of reactants within sediments (e.g. Fig. 10) (Henrichs and Farrington, 1987).

C. americanus feeds on particles captured by the tentacular crown, and transforms more or less labile organic material into relatively refractory protein structures during tube construction and maintenance. This animal must therefore contribute to the preservation of organic matter in sediments. The role of non-living, polymeric animal "tissue," such as *C. americanus* tubes, in the overall metabolic activity and nutrient dynamics in marine sediments can be assessed roughly when production and degradation rates are known.

Three basic assumptions are crucial when the impact of tubes on sediment processes are evaluated: (1) Tube production (P_T) is proportional to the secondary production of *C. americanus*. This assumption probably underestimates the true tube production, because continuous tube maintenance which counteracts decay/

disintegration processes is ignored. (2) Secondary production of *C. americanus* is equal to the annual mean biomass × 2.5. Several studies have revealed that the annual production (P) of benthic invertebrates generally is 1–4 times the mean biomass ($\overline{B}$) (Waters, 1969; Banse and Mosher, 1980). The presently chosen $P/\overline{B}$ of 2.5 is the mean of reported values. (3) Tube decay follows a simple "one-G" first-order type of reaction. If the rapid initial rate observed during tube decay is caused by a preferential decomposition of the 5% carbohydrate content, the decay pattern may be more complicated than the proposed overall first-order reaction. In that case, the decay constant of the more refractory cerianthin protein polymer will be lower than presently estimated.

The mean density of *C. americanus* at station R in Long Island Sound (May, August and October 1988) is 33.3 ± 9.8 m^{-2}. Assuming an average individual sea anemone biomass of 0.86 ± 0.20 g ww, the area specific living biomass ($\overline{B}$) is ~29 g ww m^{-2}. Based on a $P/\overline{B}$ = 2.5, the annual production of *C. americanus* would be ~72 g ww m^{-2} yr^{-1}. If tube production is proportional to sea anemone production, tubes are responsible for an input of about 87 g dw, 5.7 g POC and 1.4 g PON m^{-2} yr^{-1} to the sediment (assuming 1 g wet sea anemone tissue on average is associated with 1.2 g dw tube, at 65 mg POC g^{-1} and 15 mg PON g^{-1}). Given the first order reaction, $dG/dt = R_T = -k\,G$, where G is the sediment tube content, steady state tube content G_{ss} ($P_T = R_T$) in the sediment will be $G_{ss} = P_T/k$. By applying the above production estimate and the first-order decay constant found in the SEDTUB experiment (Table 4), the steady state contents of tube carbon and nitrogen, G_{ss}, in sediments at station R in Long Island Sound are, 26 and 14 g m^{-2}, respectively. Only 9 and 4% of this is fresh tube material immediately associated with living animals. If tube input is limited to the upper 30 cm of the sediment column and sediment POC and PON content is assumed constant within this depth interval at the level found for the subsurface sediment used in the present experiment (1.8 ± 0.1% POC; 0.22 ± 0.02% PON, porosity = 0.699), *C. americanus* tubes will account for 0.6 and 2.8%, respectively, of bulk organic carbon and nitrogen in the sediment. If tubes are focused into a smaller or larger depth interval of sediment, this contribution would change accordingly, for example, 3 times higher if a 10 cm thickness is assumed. Decay constants may also be smaller than presently estimated (likely because annual mean temperature is less than 20°C as used in the experiment and because inital rates are used), in which case these percentage contributions will be higher. Other infaunal animals will, depending on the degradability of their tube structures contribute more or less to the organic pool in sediments and thereby accentuate the influence of tubes on microbial transformations and organic matter storage.

Dead animal tissues and mucous secretion products are usually considered to be stimulatory agents for the overall microbial activity in sediments (Aller, 1982; Reichardt, 1986; Kristensen, 1988). Despite the fact that tube material is relatively refractory compared with fresh biogenic debris, decomposing *C. americanus* tubes do

stimulate microbial activity in the subsurface sediment used here. This is because sediment taken from below 10 cm contains detritus which is even more refractory than at least a portion of the tubes. Overall microbial activity and abundances are enhanced 20–40% relative to subsurface sediment devoid of tubes. Tube material deep in the sediment will provide substrate for microbial decay, some portion of which is ~10 times more reactive than the surrounding refractory detritus otherwise available.

Production of nitrogen rich cerianthin for tube construction must be a significant sink in the carbon and nitrogen balance of *C. americanus,* but also of the Long Island Sound benthos in general. The fraction of ingested food devoted to tube structures is apparently of a similar magnitude as that incorporated into living tissues (ash free dry wt/wet wt ~0.12) during growth. If 64 g C m^{-2} yr^{-1} or 31% the primary production in Long Island Sound (205 g C m^{-2} yr^{-1}) is available for benthic organisms (Riley, 1956), the production of *C. americanus* tubes consumes ~9% of the average benthic carbon supply and ~12% of the nitrogen flux (assuming Redfield source C:N ~6.7).

5. Conclusions

(1) The fibrous, leathery tubes of the common infaunal sea anemone, *Ceriantheopsis americanus,* average 1.2 g dw per g ww animal and contain ~65 mg C g^{-1} and ~15 mg N g^{-1}. Approximately 85% of the tube dry weight is occluded inorganic sedimentary particles.

(2) Despite low molar C:N ratios (~5.1) and high Rp values (~0.5) which could imply highly reactive material, the decomposition of fresh whole tubes is relatively slow over a 122 day experimental period under either oxic or anoxic conditions. Initial first-order rate constants in oxic water, anoxic water, and anoxic sediment are ~0.76, ~0.41 and ~0.22 yr^{-1} for tube carbon and ~0.2, ~0.1 and ~0.1 yr^{-1} for tube nitrogen, respectively.

(3) The comparatively low reactivity of tube material is apparently due to the molecular structure of the major fibrous component. Fibers (~2 mm long, 2–5 μm thick) are formed from specialized nematocysts, ptychocysts, and are composed of a silk-like protein copolymer: cerianthin (Mariscal *et al.,* 1977; Bishop *et al.,* 1978). These resistant fibers show little morphological evidence of degradation during initial decomposition (122 days) suggesting that the calculated decay rates most likely are maximum estimates.

(4) Although refractory, tubes are ~10 times more reactive than ambient detritus at depth in Long Island Sound sediments. The presence of tubes in subsurface sediment stimulates the background sedimentary bacterial activity and abundances 20–40% compared to sediment devoid of tubes.

(5) The steady state tube content in central Long Island Sound sediments accounts for ~0.6% and ~2.8% of the POC and PON detrital pools, respectively,

over a depth of 0–30 cm. If only the upper 10 cm is considered the figures are ~1.8% and ~8.4%, respectively. *C. americanus* tube production alone can account for ~9% of the average POC and ~12% of the PON flux to the benthos.

(6) The organic linings of tube and burrow structures formed by benthic animals may represent a significant component of the sedimentary carbon and nitrogen cycle, contributing to refractory compound formation and organic matter preservation.

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