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<thead>
<tr>
<th>Lecture No.</th>
<th>Topic</th>
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<td>Benthic generalizations</td>
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<tr>
<td>2</td>
<td>Sediment microbiology</td>
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<td>3 – 4.5</td>
<td>Basic sediment geochemistry – redox gradients; Benthic energy resources</td>
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<td>4.5 -5.5</td>
<td>Suspension feeding</td>
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<td>5.5-6.5</td>
<td>Deposit feeding</td>
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<tr>
<td>6.5-8</td>
<td>Distribution patterns: Size classes; Sediment type vs. community correlations; Pollution gradients; Depth zonation</td>
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<td>9</td>
<td>Pelagic-benthic coupling and climate change (especially at high latitudes) or Life Histories and Recruitment</td>
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<tr>
<td>10-11</td>
<td>Deep-sea reducing habitats: Hydrothermal vents; Geologic setting and global distribution; Microbial processes; Macrofaunal structure and processes; Other deep-sea reducing habitats: Subduction zones; Petroleum seeps; Whale falls</td>
</tr>
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BENTHIC GENERALIZATIONS AND MICROBIAL PROCESSES

1. Why care about benthos?

2. Benthic Generalities

3. Benthic microbial processes
   a. The organisms
   b. Standing crop
   c. Bacterial (microbial) activity

Definitions:

**Benthos** - organisms living on or in the ocean floor.

**Benthic ecology** - study of the structure and dynamics of organisms living on or in the ocean floor, and the interactions of these organisms (at individual, population and community levels) among themselves and with their environment.
Why study benthos and benthic ecology?

"I don't know why I don't care about the bottom of the ocean, but I don't."

by Saxon (New Yorker Magazine, 1983)
Fig. 2.4. Distribution of Earth's surface lying at different levels: (a) frequency distribution, (b) cumulative-frequency curve based on (a) termed the Hypsographic Curve. This should not be confused with the superficially similar profile of the continental margin shown in Fig. 2.2.
Most phyla are found in marine sediments

Dunn et al., 2008: Nature, 4/14/2008
Figure 9. Reaction rates are often a function of grain size or sediment surface area. (A) O₂ consumption by aerobic bacteria on particles and other oxidation reactions as a function of surface area. The constant slope of the relation demonstrates that the oxygen flux to a surface is constant. After Hargrave and Phillips (1977). (B) The theoretical relation between surface area per mass of sediment and particle diameter or grain size. Particles are assumed to be simple spheres of density 2.5 g/cc. Actual clay particles have considerably greater surface areas per mass, ranging from ~10–30 m²/g (Kaolinite) to 40–100 m²/g (Smeectite). Fine-grained material is therefore much more reactive than a comparable mass of coarse material with respect to surface-dependent processes such as organic matter decomposition.
PLATE 3-6. Microbial populations of sulfide sediments. (A) Patch of sulfur bacteria, containing *Beggiaota* filaments, the globular *Thiocapsa* with an *Oculatella* (trichomes), pennate diatoms, ciliates, a nematode, and four species of ciliates. (B) Surface of sulfur crust, with granular colonies of the sulfur bacteria *Lautropia*, filaments of *Beggiaota*, an *Oculatella*, pennate diatoms, large harpacticoid copepod nauplii, and eight species of ciliates. From T.M. Fenical. 1969, *Ophelia* 6:1-182.
3.5 B.Y.A. - first microbial life forms on Earth
1677 - microscope invented, marine microbes first observed
1838 - first formal binomial classification of a microbe
1970’s - discovery of Archaebacteria (*Archaea*)
1976-7 - discovery of novel microbes at deep sea hydrothermal vents
1979 - discovery of photoautotrophic bacterium *Synechococcus*
1988 - discovery of photoautotrophic bacterium *Prochlorococcus*
1992 - discovery of planktonic *Archaea*
1996 - first complete genome sequence of a marine microorganism *Methanococcus jannaschii*
1998 - discovery of novel *nif* genes at HOT/BATS stations
2000 - discovery of bacterial rhodopsin light-proton pump in SAR 86 at HOT
2000 - discovery of mesopelagic dominance of *Archaea* at HOT
2001 - discovery of novel picoeukaryotes in the marine plankton by nucleotide sequence analysis
2001 - ?

From Dave Karl
Figure 1. The Three-Domain Tree of Life Based on Small-Subunit rRNA Sequences

ARCHAEA

BACTERIA

EUCARYA

0.1 changes per nt
A marine microbial consortium apparently mediating anaerobic oxidation of methane

A large fraction of globally produced methane is converted to CO₂ by anaerobic oxidation in marine sediments. Strong geochemical evidence for net methane consumption in anoxic sediments is based on methane profiles, radiotracer experiments and stable carbon isotope data. But the elusive microorganisms mediating this reaction have not yet been isolated, and the pathway of anaerobic oxidation of methane is insufficiently understood. Recent data suggest that certain Archaea reverse the process of methanogenesis by interaction with sulphate-reducing bacteria. Here we provide microscopic evidence for a structured consortium of archaea and sulphate-reducing bacteria, which we identified by fluorescence in situ hybridization using specific 16S rRNA-targeted oligonucleotide probes. In this example of a structured archaebacterial-symbiont association, the archaea grow in dense aggregates of about 100 cells and are surrounded by sulphate-reducing bacteria. These aggregates were abundant in gas-hydrate-rich sediments with extremely high rates of methane-based sulphate reduction, and apparently mediate anaerobic oxidation of methane.

At the Cascadia convergent margin off the coast of Oregon, discrete methane hydrate layers are exposed at the sea floor, at a water depth of 600–800 m that corresponds to the hydrate stability limit. These hydrate layers are formed from gaseous methane that continuously ascends along faults generated by accretionary tectonics. The crest of the southern Hydrate Ridge (46° 34' N, 129° 48' W, 770 m water depth) is populated by large communities of clams of the genus Calyptogena, and by thick bacterial mats of the sulphide-oxidizing Beggiatoa, both of which indicate areas of active gas seeping. Undisturbed sediment cores with Beggiatoa mats were obtained using a video-guided multiple core during RV SONNE Cruise SO143-2 in August 1999 (ref. 10). These samples often released gas bubbles due to decompression during recovery.

Sulphate reduction rates (SRRs) were extremely high in sediments covered by Beggiatoa mats, reaching more than 5 μmol cm⁻² d⁻¹ in the surface sediments (Fig. 1). Integrated over the upper 15 cm, the resulting SRR is 140 mmol m⁻² d⁻¹, this is, to our knowledge, the highest value ever measured in cold marine sediments. At a nearby reference station without gas hydrates and vent colonization, SRRs were below the detection limit (<1 nmol cm⁻² d⁻¹). Thus, at Hydrate Ridge, sulphate reduction is clearly fuelled by high methane fluxes from below, while organic deposition from surface waters is not a significant substrate source for sulphate-reducing bacteria (SRB). A similar phenomenon was observed at gas seeps in the Gulf of Mexico, where 600-fold higher SRRs were measured at methane seeps (up to 2.5 μmol cm⁻² d⁻¹), calculated from sulphate concentration profiles compared to reference stations. The restriction of such high SRRs to sediments rich in methane is evidence for a direct link between the processes of methane and sulphate turnover. Sulphate has been proposed to be the terminal electron acceptor in the zone of anaerobic oxidation of methane, according to:

\[ \text{CH}_4 + \text{SO}_4^{2-} \rightarrow \text{HCO}_3^- + \text{HS}^- + \text{H}_2\text{O} \] (1)

Assuming this stoichiometry, the turnover of methane can exceed 5 mmol m⁻² d⁻¹ in the sediments of the Hydrate Ridge, where a dissolved methane concentration of 80 mM is reached above decomposing gas hydrates at in situ temperature (4°C) and hydrostatic pressure (8 MPa). As one product of anaerobic oxidation of methane, sulphide accumulates to concentrations almost equivalent to those of sulphate consumed (Fig. 1). Intense sulphide production...
DeLong, 2000


In situ identification of archaea/SRB aggregates with fluorescently labeled rRNA-targetted oligonucliotide probes; Archaea = red, SRB = green, white images are DAPI (DNA) stained. Boetius et a. (2000).

E.g., of product-substrate coupling causing metabolic zonation

Anaerobic Oxidation of Methane by Microbial Consortium
Figure 1. Bacterial colonization of surfaces. When three bacterial species are present as planktonic cells, a single species may adhere \((A_1)\) and proliferate to form a glycocalyx-enclosed single-species microcolony \((A_2)\) that constitutes a locus both chemically and physically different from the uncolonized surface. Alternatively, the primary colonizer may attract secondary colonizers of other species \((B_1\) and \(C_1)\). They may proliferate to form mixed microcolonies with mixed glycocalyx matrices \((B_2\) and \(C_2)\) within which ion binding \((B_3)\) or the production of metabolites such as organic acids \((C_3)\) may produce surface loci even more radically different from the uncolonized surface.

Figure 4. Corrosion potentials caused by biofilms. With the metabolic activity of aerobic and facultative organisms in the upper biofilm, the lower biofilms can become anaerobic, allowing microcolonies of anaerobic organisms to develop on the metal surface. Corrosion currents can be measured between surface areas affected by metal cation-binding exopolysaccharides \((B_3)\) or between surface areas made acidic \((pH\ 5.5)\) by organic acid generation in adherent microcolonies \((C_3)\). These chemical and physical surface heterogeneities can then be amplified by progressive growth of either type of bacteria until definite anodes and cathodes are established and corrosion pitting has been initiated at the anode. Once initiated, these corrosion pits can penetrate 5/8-inch-thick steel within 6 months.

Costerton and Lappin-Scott, 1989
The ecological implications of body size

Figure 3.2. Specific metabolic rates of homeotherms, poikilotherms, and unicells (Equations 3.4–3.6). The proportion of the energy reserves used per day (right axis) was calculated as specific metabolic rate ($J \cdot s^{-1}$) times 86,400 s d$^{-1}$ divided by $7 \times 10^6$ J kg$^{-1}$ fresh mass.
### Table 1.3. The two types of phototrophic metabolism

<table>
<thead>
<tr>
<th>type</th>
<th>electron donor</th>
<th>carbon source</th>
<th>examples</th>
</tr>
</thead>
<tbody>
<tr>
<td>photolithotrophy</td>
<td>$\text{H}_2\text{O}$</td>
<td>$\text{CO}_2$</td>
<td>plants, blue-green bacteria</td>
</tr>
<tr>
<td>(= photoautotrophy)</td>
<td>$\text{H}_2\text{S}, \text{S}^0, \text{H}_2$</td>
<td>$\text{CO}_2$</td>
<td><em>Chromatiaceae</em>, <em>Chlorobiaceae</em></td>
</tr>
<tr>
<td>photoorganotrophy</td>
<td>organic substrates</td>
<td>organic substrates</td>
<td><em>Rhodospirillaceae</em></td>
</tr>
</tbody>
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### Table 1.4. The two types of chemotrophic metabolism

<table>
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<th>electron donor</th>
<th>electron acceptor</th>
<th>carbon source</th>
<th>examples</th>
</tr>
</thead>
<tbody>
<tr>
<td>chemoorganotrophy</td>
<td>organic substrate</td>
<td>$\text{O}_2$</td>
<td>organic substrate</td>
<td>pseudomonads, bacilli</td>
</tr>
<tr>
<td>(= heterotrophy)</td>
<td>organic substrate</td>
<td>$\text{NO}_3^-$</td>
<td>organic substrate</td>
<td><em>Bacillus licheniformis</em></td>
</tr>
<tr>
<td></td>
<td>organic substrate</td>
<td>$\text{SO}_4^{2-}$</td>
<td>organic substrate</td>
<td>sulfate reducers</td>
</tr>
<tr>
<td></td>
<td>organic substrate</td>
<td>organic substrate</td>
<td>organic substrate</td>
<td>clostridia, lactic acid bacteria</td>
</tr>
<tr>
<td>chemolithotrophy</td>
<td>$\text{H}_2$</td>
<td>$\text{O}_2$</td>
<td>$\text{CO}_2$</td>
<td>hydrogen-oxidizing bacteria</td>
</tr>
<tr>
<td>(= chemoautotrophy)</td>
<td>$\text{H}_2\text{S}$</td>
<td>$\text{O}_2$</td>
<td>$\text{CO}_2$</td>
<td>thiobacilli</td>
</tr>
<tr>
<td></td>
<td>$\text{H}_2\text{S}$</td>
<td>$\text{NO}_3^-$</td>
<td>$\text{CO}_2$</td>
<td><em>Th. denitrificans</em></td>
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<tr>
<td></td>
<td>$\text{Fe}^{2+}$</td>
<td>$\text{O}_2$</td>
<td>$\text{CO}_2$</td>
<td><em>Th. ferroxidans</em></td>
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<tr>
<td></td>
<td>$\text{NH}_3$</td>
<td>$\text{O}_2$</td>
<td>$\text{CO}_2$</td>
<td>Nitrosomonas</td>
</tr>
<tr>
<td></td>
<td>$\text{NO}_2^-$</td>
<td>$\text{O}_2$</td>
<td>$\text{CO}_2$</td>
<td>Nitrobacter</td>
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<tr>
<td></td>
<td>$\text{H}_2$</td>
<td>$\text{CO}_2$</td>
<td>$\text{CO}_2$</td>
<td>methanogenic bacteria</td>
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<tr>
<td></td>
<td>$\text{H}_2$</td>
<td>$\text{CO}_2$</td>
<td>$\text{CO}_2$</td>
<td><em>Acetobacterium</em></td>
</tr>
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</table>
Fig. 8-7. Postulated roles for bacteria in the sea. The various bacterial reactions and reaction products are outlined. The contribution of the prokaryotes to primary productivity is thought to be extremely small in comparison with the eukaryotic photosynthesis. Probably it is insignificant in the open oceans where nutrients are generated that directly affect the water-column dynamics. For the other reactions, while the reactions are documented, the magnitudes of the rates are generally unknown.

Now known not to be true
Sediment Microbes are also major producers of DOC

1) The initial degradative steps through in the remineralization of the sediment OC by the microbial community limits the overall remineralization process (Westrich & Berner, 1988).

2) LMW-DOC compounds can be used by the terminal respiratory organism because bacterial can transport compounds smaller than ~600 daltons across their cell walls (Weiss et al. 1991).

3) During the fermentation, reduce H2 is often important end-product, along with CO2 and organic acids and alcohols of intermediate oxidation states (ethanol). Much of H2 is consumed by terminal respiratory processes, e.g. sulfate reduction or methanogenesis (last lecture). H2 is also consumed by homoacetogens, which live autotrophically by reducing CO2 to acetate using H2 (Fenchel et al. 1998).

4) Competition for acetate, formate, and H2 control the relative importance of sulfate reduction and methanogenesis in many anoxic sediment. In high concentration, sulfate reduction and methanogenesis can occur simultaneously (Winfrey & Zeikus, 1977; Crill & Martens, 1986).

(Summary by Guangyi Wang)

Depth (relative to sed.-water interface)

Data composite from a number of papers including:
- Meyer-Reil, 1987
- Smith et al., 1986

Deep Sea - e.g., 3800m NE Pacific

Shallow water - e.g., Kiel Bight 18m

Bacterial #/ml - Direct Counts

\[ 10^4 \quad 10^5 \quad 10^6 \quad 10^7 \quad 10^8 \quad 10^9 \]
Bacterial abundances as a function of subbottom sediment depth as seen in ODP boreholes down to ~750mbsf.

(from Parkes, Cragg & Wellsbury, 2000)

Mean annual depth profiles of microbial domains in the north Pacific subtropical gyre

(from Karner et al., 2001)

Bacterial abundances as a function of subbottom sediment depth as seen in ODP boreholes down to ~750mbsf.

(from Parkes, Cragg & Wellsbury, 2000)
FIG. 4.—Localised distribution of micro-organisms and surface material on an intertidal sand grain
Table 5. Comparison of available area of sediment surface per bacterium in different habitats.

<table>
<thead>
<tr>
<th>Sediment Type</th>
<th>Habitat</th>
<th>μ² per Bacterium</th>
<th>Source</th>
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<tbody>
<tr>
<td>Fine silt</td>
<td>Marine intertidal</td>
<td>411</td>
<td>This study</td>
</tr>
<tr>
<td>Coarse silt</td>
<td>Marine intertidal</td>
<td>130</td>
<td>This study</td>
</tr>
<tr>
<td>Fine sand</td>
<td>Marine intertidal</td>
<td>377</td>
<td>This study</td>
</tr>
<tr>
<td>Pebbles</td>
<td>Marine</td>
<td>300</td>
<td>Battaglini &amp; Anthony (1971)</td>
</tr>
<tr>
<td>Clay-silt</td>
<td>Lacustrine</td>
<td>311</td>
<td>Tsoemogou &amp; Anthony (1971)</td>
</tr>
<tr>
<td>Pebbles</td>
<td>Lacustrine</td>
<td>294</td>
<td>Potter (1964)</td>
</tr>
</tbody>
</table>

greater the adsorptive surface area for organic matter. However, this relationship could be expected as well from hypotheses B and C above. E. Where total organic content is highest, both nitrogen and organic carbon will tend to reach their maxima. F. As with organic carbon, high adsorptive capacity of fine materials can lead to accumulation of both organic and inorganic nitrogen.

Dale, 1974
Microbial Growth Rates and Biomass Production in a Marine Sediment: Evidence for a Very Active but Mostly Nongrowing Community

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Received 1 April 1987; Accepted 9 July 1987

Biomass, nucleic acid synthesis, and specific growth rates of the microbial communities were measured throughout a vertical profile of a coastal marine sediment. The microbial biomass, as determined by ATP concentrations, in the sediment-water interface was over twice that measured in the other horizons of a 10-cm profile. Likewise, biomass carbon production, as determined by DNA synthesis, and the specific growth rate, as determined from the kinetics of [3H]-ATP pool labelling, were also elevated at the interface. These results indicate that, due to a large and active community in the interface, the greatest amount of microbial activity, growth, and biosynthesis occurs within the first few millimeters of sediment. These results notwithstanding, a combination of two independent techniques established that over 90% of the sediment-water interface community was not actively growing.

Individual microbial cells in a natural environment are either growing or nongrowing. It would seem to be an easy task to differentiate the two groups, but this has not been the case. Simple culturing techniques have not been able to duplicate the complex physical and chemical parameters of most natural environments. Since many determinations of microbial activity, productivity, and specific growth rate depend on measuring or estimating the magnitude of the living community, the accuracy of this estimation is crucial for assessing the role of microbes in natural environments.

The problem is particularly complex in marine sediments, where the microbial community often exceeds 10^9 cells per g (2, 12). With such a large total population, even a small percentage of it would represent a substantial number of individuals. While several studies (9, 11, 17, 19) have measured the number of metabolically active individuals within the community, to my knowledge no studies have attempted to determine the proportion of nongrowing cells in any marine environment.

In an attempt to characterize the growth of microorganisms in a marine sediment, I used several techniques to measure specific microbial growth rates and biomass production in the surface sediments of Halifax Harbor. In addition, by combining a recently developed technique (5a) with direct microscopic enumeration and a sediment incubation method that I developed earlier (12), I report here the first calculation of the magnitude of the nongrowing portion of the microbial community in a natural environment.

MATERIALS AND METHODS

Sampling site and sample collection. The sampling site used in this study was the area of Halifax Harbor known as Eastern Passage, which was also the site of previous studies (7, 11, 12, 16). Samples of sediment were collected in plastic core tubes by hand by scuba divers, as described previously (11). Once collected, the sediment cores were transported on ice to the laboratory. Due to the proximity of the sampling site to the laboratory, experiments were begun within 1 h of sample collection. The sediment-water interface layer was removed by aspiration as described previously (11). Once the interface was removed, the overlying water was carefully decanted and the sediment was extruded vertically by forcing a rubber plug through the bottom of the core tube. When 1 cm of sediment was extruded, it was removed with a spatula, and the process was repeated until 2.1 cm horizons had been collected. Unsealed sediment was then used directly (sediment plug) or suspended in filter-sterilized bottom water to yield a sediment slurry containing approximately 2.5 mg (dry weight) of sediment per ml of slurry.

ATP determinations. Sediment plugs (2 cm) were placed directly into 10 ml of cold 1.47 M H3PO4 and vigorously mixed. After an extraction period of 10 min, the samples were centrifuged and 0.1 ml of the supernatant was diluted into 4.9 ml of phosphate buffer (60 mM, pH 7.4) and assayed for ATP by the methods of Karl and Craven (5). For interface and other slurry samples, 1 ml of the slurry was pipetted directly into 5 ml of boiling 60 mM phosphate buffer and extracted at 100°C for 5 min. For water samples, 100 to 250 ml of water was filtered through a Whatman GF/F glass fiber filter. Immediately after filtration, the filter was placed into boiling buffer and extracted as described for interface samples. Internal ATP standards were used to correct for real and apparent losses of extractable ATP.

Nucleic acid synthesis rates. DNA and RNA synthesis rates were determined by using 30-ml portions of the sediment slurries. [2-3H]Thymidine (specific activity, 17.1 Ci/mmol) was added to the slurries to a final concentration of 133 nCi/ml, and the samples were incubated with gentle shaking at the in situ temperature of 2°C in a Photokres (New Brunswick Scientific Co.) incubator. During the incubation and sampling period, the headspace over the slurries was continuously gassed with a mixture of nitrogen, oxygen, and carbon dioxide to maintain the slurry at the in situ O2 concentration (9). At various times duplicate 1-ml subsamples were injected into 10 ml of cold 1 N HCl containing nonradioactive adenine (2 mg/ml). The tubes were then capped and frozen. Radioactive RNA and DNA were separated and measured by the method of Karl (5) as adapted for sediment samples by Craven and Karl (1). The specific radioactivity of the ATP pool was measured at each time point by injecting a 0.2-ml portion of the sediment slurry into 5 ml of boiling phosphate buffer (60 mM, pH 7.4), followed by sample concentration.
TABLE 1. Specific growth rates and generation (doubling) times for the microbial community in the sediment-water interface of Halifax Harbor

| Date (mo-day-yr) | DC | AT | % Nongrowing
<table>
<thead>
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<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\mu$ (h$^{-1}$)</td>
<td>SE</td>
<td>Doubling time (h)</td>
</tr>
<tr>
<td>10-10-85</td>
<td>0.0069</td>
<td>$9.3 \times 10^{-5}$</td>
<td>100</td>
</tr>
<tr>
<td>12-17-85</td>
<td>0.0037</td>
<td>$3.2 \times 10^{-3}$</td>
<td>187</td>
</tr>
<tr>
<td>12-17-85 (autoradiography)</td>
<td>0.0140</td>
<td>$2.9 \times 10^{-3}$</td>
<td>49.5</td>
</tr>
</tbody>
</table>

* Determined by comparing the two growth rates with the relationship described by Fig. 5.

---

FIG. 2. Biomass carbon production in surface sediments as extrapolated from the incorporation of [$^3$H]adenine into DNA. The hatched bars represent the mean of three determinations; the vertical bars represent the standard error of the mean.
Dissolved organic carbon concentrations in marine pore waters
determined by high-temperature oxidation

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Daniel C. McCorkle
Department of Geology and Geophysics, Woods Hole Oceanographic Institution

Abstract
We have developed sampling methods and an analytical system to determine the concentration of dissolved organic C (DOC) in marine pore waters. Our analytical approach is a modification of recently developed high-temperature, Pt-catalyzed oxidation methods; it uses chromatographic trapping of the DOC-derived CO₂, followed by reduction to CH₄ and flame ionization detection. Sampling experiments with nearshore sediments indicate that pore-water separation by whole-core squeezing causes artificially elevated DOC concentrations, while pore-water recovery by sectioning and centrifugation does not appear to introduce DOC artifacts. Results from a set of northwestern Atlantic continental slope cores suggest that net DOC production accounts for >50% of the organic C that is recycled at the sediment–water interface.

Dissolved organic C (DOC) is an abundant, but poorly understood component of the pore waters of marine sediments. Previous pore-water studies of both deep-sea and nearshore locations consistently found high concentrations of DOC in the top few centimeters of the sediments (e.g., Suess et al. 1980; Sholokovitz and Mann 1984; Heeggie et al. 1986, 1987). The measured interfacial DOC gradients determined in these studies ranged from a minimum of 50% of the gradient of metabolically derived dissolved inorganic C (DIC) in a nearshore location to >5 times the DIC gradient in sediments of the northwest Atlantic continental rise. If these measurements are correct and if the effective diffusivity of pore-water DOC is even 10% of that of DIC (e.g., Mackin 1986; Cornet et al. 1986; Burdige et al. 1992), then DOC must be a quantitatively significant product of organic matter degradation in surficial marine sediments. Pore-water DOC may also be significant in the stable carbon isotope budget of surficial marine sediments. Several studies have shown an imbalance in this budget, with the DIC flux across the sediment–water interface richer in ¹³C than can be explained by its sedimentary sources (McCorkle et al. 1985; Sayles and Curry 1983; McArthur 1989; McNichol et al. 1991). A flux of ¹³C-depleted DOC (e.g., Alperin 1988) could resolve this imbalance.

Clean, artifact-free sampling procedures and a precise, well-calibrated analytical method are prerequisites for determining the role of DOC in the benthic C cycle. We have modified existing high-temperature, Pt-catalyzed oxidation techniques (Sugimura and Suzuki 1988) to measure both the concentration and C isotopic composition of pore-water DOC and have carried out comparisons of centrifugation and whole-core squeezing methods. In this paper, we describe our sampling procedures and DOC oxidation method and present initial results of pore-water DOC from the northwest Atlantic continental slope.

Acknowledgments
We appreciate the assistance of J. Lee and J. Goodreau in the lab and at sea. We are grateful to N. Frew, who provided the Vineyard Sound and NW Atlantic surface samples that we used to examine instrument blanks, and to F. Sayles, who provided unpublished data. The manuscript benefited from reviews by F. Sayles, H. Edmonds, D. Burdige, and an anonymous reviewer.

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Woods Hole Oceanographic Institution Contribution 8173.

1464
Laboratory study of disturbance in marine sediments: response of a microbial community


Department of Biological Sciences, Florida State University, Tallahassee, Florida 32306, USA

ABSTRACT: Disturbance has been shown to be an important component of the ecology of soft-bottom macrobenthic and megabenthic marine communities. Its importance in the ecology of microbial communities was investigated by using sieving of marine sediments as a controlled disturbance. Following the disturbance, sediments were maintained in microcosms. Using a suite of biochemical measures, sieving was found to influence microbial biomass, community structure, and metabolic activity. Sieving caused an immediate decrease in microbial growth rates and a shift in metabolic status towards the synthesis of phospholipid. Microbial biomass was initially unaffected. Several hours later, growth rates increased and biomass had decreased by 75%. Microbial biomass returned to pre-disturbance levels 8 h after sieving. Groups of phospholipid, fatty acids, and phospholipid fatty acids, each associated with different functional groups of microorganisms, varied in their response to sieving. This result suggested that components of the microbial community differed in their reaction to this disturbance. Ambient sediments collected at the time of the construction of the microcosms were contrasted with sediments maintained in the laboratory microcosms for 5 d. Laboratory conditions significantly altered the microbial community structure and growth rates were significantly lower. Measures of metabolic status indicated that some of the microorganisms were stressed. This study demonstrates the potential significance of disturbance in the ecology of the benthic microbial community and that uncoupling sediment from the bion and abiotic influences of the environment significantly affects the composition and activity of the microbial community.

INTRODUCTION

Sedimentary bacteria live in a physically and chemically complex environment and numerous factors have been shown to influence their distribution. Microscopic analysis indicates that marine sediments are a heterogeneous environment of organic and inorganic particles of various sizes, bridged, or encompassed, by an organic matrix (Frankel & Mead 1973, Watling 1988). Sediment grain size, the mineral nature of the grains, and the microtopography of the grains have been shown to influence the bacterial biomass in marine sediments (Meadows & Anderson 1967, Dale 1974, Weise & Rheinheimer 1978, Nickels et al. 1981, DeLaunay & Mayer 1983). In shallow waters, deposition rates of detrital carbon are high and the majority of the decomposition of detritus occurs in the sediments (Suess 1975). The major, early diagenetic reactions result from microbiological decomposition of organic matter (Berner 1976), and this activity produces many complex gradients within the sediments which in turn affect the distribution and metabolic activities of the bacteria there (Jones 1979).

Most, but not all, marine sediments are inhabited by macrobenthos and their activities profoundly affect the physical and chemical nature of the sediments. Burrowing for shelter or food and ingestion of sediment disturbances caused by biological agents and henceforth referred to as biotic disturbance - cause changes in the grain size, sorting, fabric, water content and compaction of the sediments (for reviews see Gray 1974, Roests 1974, Aller 1978, Roests & Boyer 1982). Biotic disturbance also affects diagenetic reactions and the pore-water profiles of reactants and products (Aller 1982). Sandy sediments may have very high rates of biotic disturbance with turnover rates of 0.7 to 4 d for...
Fig. 2. Effect of ray feeding on (A) short-term metabolic status, (B, C) growth rates and (D, E, F) biomass of an estuarine sedimentary microbial community. (●) Ambient sediment; (□) tailings zone sediments; (○) sediments from the bottom of the ray feeding pits. Zero hours represents the start of the sampling period. Ray feeding was unobserved, but was estimated to have occurred 3 to 5 h before the start of the experiment. Units, standard deviations and statistical analyses are given in Tables 1 and 2.