

Dissolved organic matter in abyssal sediments: Core recovery artifacts

Per O. J. Hall,¹ Jenny Brunnegård, and Gustaf Hulthe²

Department of Chemistry, Marine Chemistry, Göteborg University, SE-412 96 Göteborg, Sweden

William R. Martin

Department of Marine Chemistry and Geochemistry, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543

Henrik Stahl³ and Anders Tengberg

Department of Chemistry, Marine Chemistry, Göteborg University, SE-412 96 Göteborg, Sweden

Abstract

We report measurements of pore-water dissolved organic carbon (DOC), dissolved organic nitrogen, total dissolved carbohydrates, dissolved free monosaccharides, and ammonium in recovered deep-sea sediments from the Porcupine Abyssal Plain (PAP), Northeast Atlantic. There were distinct maxima close to the sediment–water interface of these constituents at all times of the year. The very high diffusive effluxes calculated from these pore-water distributions were not compatible with simultaneous sediment trap measurements of particulate organic carbon, nitrogen, and carbohydrate fluxes toward the seafloor. Effluxes calculated from pore-water DOC distributions in recovered cores from another Atlantic deep-sea site, showing almost identical maxima as those at PAP, were more than an order of magnitude greater than simultaneous in situ chamber DOC flux measurements. We suggest that the dissolved organic matter maxima are predominantly artifacts induced by lysis of, or leakage from, mainly bacterial biomass resulting from decompression and/or warming during recovery of the sediment cores from the abyssal seafloor. Temperature elevation during core recovery from the abyss gives a N₂ saturation of about 150%, and the combined effect of warming and decompression results in a CO₂ saturation of about 135%, which together plausibly are associated with bubble formation creating cell bursting. Previous estimates of microbial biomass in abyssal sediments may be underestimates because of the difficulty of counting lysed bacterial cells. Since exoenzymes are inducible, previous measurements of their activities in recovered abyssal sediments may be overestimates.

¹ Corresponding author (perhall@chem.gu.se).

² Present address: AstraZeneca R&D, SE-431 83 Mölndal, Sweden.

³ Present address: Marine Biological Laboratory, University of Copenhagen, Strandpromenaden 5, DK-3000 Helsingør, Denmark.

Acknowledgments

We thank A. Rice and D. Billet, coordinators for the BENGAL project and chief scientists on several cruises; M. Priede, coordinator for the ALIPOR project and chief scientist on the D222 and D236 cruises; O. Pfannkuche for inviting us to participate on the Meteor M42/2 cruise; A. Gooday for helping with the multiple corer sampling; S. Hulth for assistance during the D222 cruise; R. Jahnke for providing the coring instrument that was used to collect pore-water samples on the Ceara Rise and for providing samples from his in situ benthic flux chambers; C. Sweeney for assistance with sampling and DOC analyses; and the captains and crew of the RV *Discovery*, FS *Meteor*, and RV *Challenger* for skillful work during expeditions. Interpretations and arguments presented in this paper benefited from communication with J. Aller, R. Aller, L. Anderson, W. Berelson, R. Jahnke, K. Lochte, and K. L. Smith. Constructive criticism on the submitted manuscript from W. Berelson and an anonymous reviewer improved the paper.

Financial support for this study was provided by the European Commission under the EU-MAST III program, Contract MAS3-CT950018 (project BENGAL) and Contract MAS3-CT950010 (project ALIPOR); by the Swedish Natural Science Research Council (NFR); and by the U.S. National Science Foundation (NSF) under grant OCE-9810962.

The deep-sea floor (water depth greater than 2,000 m) covers almost 60% of the surface of the planet Earth. Sediments of the deep-sea floor contain a reservoir of reactive organic matter and they contain a tremendous number of microorganisms and invertebrates capable of turnover and degradation of this reactive material (e.g., Deming and Yager 1992; Smith 1992; Jahnke 1996). Studies have been undertaken to constrain the role of deep-sea sediments in the recycling of particulate biogenic material in the ocean and to quantify the deposition of such material from overlying waters. One important tool in such studies is the determination of solute distributions in sediment pore waters.

Discrepancies have been observed in deep-sea sediments between pore-water solute distributions obtained in situ and onboard ship. Among the earliest observations are those of total carbonate (or dissolved inorganic carbon, DIC) and alkalinity in pore waters of the Pacific (e.g., Murray et al. 1980) and of the Atlantic (Sayles 1981). Alkalinity and DIC concentrations near the sediment–water interface were found to be clearly lower in cores onboard ship than corresponding in situ values, and it was suggested that CaCO₃ precipitated in the box core samples when they were brought from the ocean depths to atmospheric pressure.

Oxygen penetration depths have been found to be shallower and pore-water gradients steeper in surface-retrieved

cores than in situ (Glud et al. 1994, 1999; Epping et al. 2002). Clear near-surface peaks of ammonium in surface processed cores were not found in situ (Berelson et al. 1990; Glud et al. 1994; Aller et al. 1998). Differences between in situ and ex situ distributions have also been observed for nitrate (Hammond et al. 1996; Martin and Sayles 1996; Aller et al. 1998), silicate (Fanning and Pilson 1971; Jahnke et al. 1989; Aller et al. 1998), and urea (Epping et al. 2002). In most cases, ex situ nitrate and silicate distributions exhibited steeper near-surface gradients and shallower nitrate penetration depths than in situ distributions. Urea concentrations were found to be significantly enhanced ex situ when compared to in situ levels. Also, deep-sea benthic oxygen fluxes measured in situ with chambers have been found to be lower than corresponding onboard incubations (Smith and Hinga 1983; Reimers et al. 1986; Glud et al. 1994), a result that is consistent with the observed differences between in situ and ex situ oxygen pore-water distributions.

Apart from the decompression effect on CaCO_3 solubility, as described above, explanations for the observed differences include stimulation of biological activity due to temperature elevation; lysis of barophilic and psychophilic microbial biomass as a result of decompression and/or warming leading to enhanced availability of fresh substrates stimulating microbial oxygen consumption and subsequently denitrification; and expulsion of pore water as a result of decreased hydrostatic pressure (Glud et al. 1994; Aller et al. 1998). Epping et al. (2002) suggested that the discrepancies presumably were a result of lysis or exudation of oxidizable substrates by infauna upon sediment retrieval on deck. However, it is not clear why infauna, and not other organisms, were proposed to be the source of the discrepancies. While explanations given to date are reasonable, they are speculative, and no firm experimental evidence supporting these explanations has so far been presented.

While we are not aware of any previous measurements of dissolved organic nitrogen (DON), total dissolved carbohydrates, or dissolved free monosaccharides in pore waters of deep-sea sediments, measurements of dissolved organic carbon (DOC) in such pore waters have been made in the Pacific (e.g., Suess et al. 1980; Burdige et al. 1999), in the Atlantic (e.g., Heggie et al. 1987; Martin and McCorkle 1993; Papadimitriou et al. 2002), and in the Southern Ocean (Hulth et al. 1997). Most of these studies reported very high DOC fluxes (calculated from pore-water gradients in recovered cores or from core incubations onboard ship), which often were 1.5–4 times higher than organic carbon oxidation rates. These previous investigations did not conclude any recovery artifacts with their DOC pore-water distributions.

We here report measurements from six cruises of pore-water DOC, DON, total dissolved carbohydrates, dissolved free monosaccharides, and ammonium in recovered sediments from the Porcupine Abyssal Plain (PAP), Northeast Atlantic. During all cruises and regardless of season, we observed distinct maxima close to the sediment–water interface of these pore-water constituents. Comparison of fluxes calculated from pore-water DOC distributions in

recovered cores, exhibiting almost identical maxima, with simultaneous in situ chamber DOC flux measurements at another Atlantic deep-sea site, is also reported. Evidence is presented that strongly indicates that these dissolved organic matter maxima predominantly are artifacts and are produced by lysis of, or leakage from, mainly bacterial biomass as a result of decompression and/or warming during recovery of the sediment cores from the abyssal seafloor. Our findings also constitute direct experimental evidence confirming some of the previous speculative explanations for the observed discrepancies between ex situ and in situ oxygen and nutrient pore-water distributions.

Materials and methods

Study site—Studies were carried out on the PAP in the Northeast Atlantic within the EU-MAST III project BENGAL (high-resolution temporal and spatial study of the Benthic biology and Geochemistry of a north-eastern Atlantic abyssal Locality). This site has a flat topography and was chosen partly because it experiences relatively little influence from the continental slope. Previous studies conducted at this site (e.g., Billett et al. 1983) have shown a strong seasonality in the deposition of organic matter on the seafloor. Primary production in the overlying water has been estimated to measure approximately $195 \text{ g carbon (C) m}^{-2} \text{ yr}^{-1}$, and the winter mixed layer lies at approximately 500 m depth. The water depth is $\sim 4,850 \text{ m}$ at the central PAP station ($48^\circ 50' \text{ N}$, $16^\circ 30' \text{ W}$), and the sediment is composed of calcareous ooze with a median grain size of 8 to $8.6 \mu\text{m}$. Sedimentary organic carbon and nitrogen contents in the mixed layer measure 0.2–0.6% (Ståhl et al. 2004b) and 0.05–0.07% (Brunnegård et al. 2004) of dry weight, respectively. Altogether six cruises to the PAP site were accomplished between August 1996 and May 1999 (Table 1).

Studies were also carried out at the base of the Ceara Rise in the western tropical Atlantic Ocean, at a water depth of 4,675 m (Table 1). Surface sediments at this site contain 0.6% organic matter and 36% CaCO_3 (Martin et al. 2000). The sedimentary oxygen consumption rate is $0.44 \text{ mmol m}^{-2} \text{ d}^{-1}$ (Jahnke and Jahnke 2004). Pore-water, microelectrode profiling, and in situ benthic flux chamber results from this location are discussed in Martin and Sayles (1996) and Jahnke and Jahnke (2004).

Sediment sampling and pore-water extraction—Sediment cores to determine pore-water distributions of DOC, DON, ammonium, total dissolved carbohydrates, and dissolved free monosaccharides at PAP were mainly collected using a multiple corer and were sometimes collected by taking subcores from the sediment brought to the surface by the chambers of the Göteborg benthic lander (Ståhl et al. 2004b; Tengberg et al. 2004). The multiple corer (MUC) cores were collected within the central coring position at PAP. Ascent rate of the multiple corer was approximately 30 m min^{-1} and ascent rate of the lander was 70 m min^{-1} . Plexiglas core tubes (10-cm inner diameter) were used. Cores having a seemingly undisturbed surface were rapidly

Table 1. Cruises, stations, dates, positions and water depths for collection of sediment with a multiple corer (MUC) or from the chambers of the Göteborg lander (Lander) at PAP and Ceara Rise. The pore-water (pw) measurements made at each station are indicated. At the Ceara Rise, benthic DOC flux was also measured in situ using the chamber lander described by Jahnke and Christiansen (1989).*

Cruise ID	Station ID	Date	Lat (N)	Long (W)	Depth (m)	Gear	pw measurements
D222	12926#2	20 Aug 1996	48°50.05'	16°16.19'	4,802	MUC	NH ₄
D226	13077#25	18 Mar 1997	48°55.96'	16°33.68'	4,825	MUC	DOC, NH ₄ , Carb
D226	13077#90	27 Mar 1997	48°49.56'	16°29.73'	4,846	MUC	DOC, NH ₄ , Carb
D226	13077#96	28 Mar 1997	48°48.56'	16°20.40'	4,846	MUC	DOC, NH ₄ , Carb
D226	13078#10	31 Mar 1997	48°58.02'	16°25.03'	4,847	MUC	DOC, NH ₄ , Carb
D231	13368#4	3 Mar 1998	48°49.95'	16°2.94'	4,814	MUC	DOC, NH ₄
D231	13368#45	16 Mar 1998	48°48.18'	16°26.62'	4,810	MUC	DON, NH ₄
D231	13368#57	21 Mar 1998	48°55.20'	16°33.20'	4,841	MUC	DON, NH ₄
M42/2	381#1	3 Aug 1998	48°56.05'	16°35.05'	4,813	Lander	DOC, NH ₄
M42/2	397#1	4 Aug 1998	48°56.01'	16°35.01'	4,811	MUC	DOC
M42/2	425#1	15 Aug 1998	48°59.54'	16°25.49'	4,812	MUC	DOC
M42/2	432#1	17 Aug 1998	48°58.01'	16°28.02'	4,810	MUC	DOC, DON
M42/2	433#1	17 Aug 1998	48°48.04'	16°27.95'	4,807	MUC	DOC, NH ₄
D236	98#11	30 Aug 1998	48°51.41'	16°29.85'	4,800	MUC	NH ₄
D236	98#16	1 Sep 1998	48°51.48'	16°29.92'	4,800	MUC	DON
Ch142	54901#13	1 May 1999	48°49.40'	16°25.10'	4,839	MUC	DOC
Ch142	54904#1	3 May 1999	48°49.10'	16°31.50'	4,840	MUC	DON, NH ₄
	Ceara Rise	Mar 1994	6°10.00'	42°53.00'	4,675	MUC	DOC
	Ceara Rise	Mar 1994	6°10.00'	42°53.00'	4,675	Lander	In situ DOC flux

* Lat, latitude; Long, longitude; Carb, total dissolved carbohydrates and free dissolved monosaccharides.

brought to a constant temperature room at +2–4°C (i.e., close to the in situ bottom-water temperature of +2.6°C) onboard ship. All procedures to obtain pore water were performed at this temperature. The temperature of water overlying the sediment in the core tubes was occasionally measured; the available measurements indicated a temperature of approximately 10–12°C in summer (lower in winter) after handling on deck and just before the cores were brought into the constant temperature room. The overlying bottom water in each core was sampled approximately 10 cm above the sediment surface and then carefully siphoned off. Ambient bottom water was also sampled from CTD/Rosette casts approximately 5 m above bottom as well as from syringes (outside chambers) on the Göteborg lander approximately 2 m above bottom. Cores were sectioned in 0.5-cm slices down to 2 cm in depth, followed by 1-cm slices down to 6 cm in depth, and finally 2-cm slices down to 20 cm in depth. Each slice was visually inspected, and large animals, which were only occasionally found, were carefully removed with a clean pair of tweezers. The sediment was placed into clean 50-mL polypropylene centrifuge tubes and gently centrifuged at 2,000 rpm (~670 × g) for 30 min at in situ temperature in a cooled centrifuge. Blank tests have shown that these tubes do not add DOC nor scavenge it from seawater (Martin and McCorkle 1993). After centrifugation supernatants were drawn into a cleaned plastic polypropylene syringe followed by filtration through a disposable cellulose acetate filter (0.45- μ m pore size). These filters were rinsed prior to use with at least 60 mL of ultrapure MQ water or bottom water; this procedure has been shown to be necessary to avoid DOC contamination from the filters (Hulth et al. 1997) as well as dissolved carbohydrate contamination (this study). DOC samples were stored at in situ temperature for

up to 24 h in clean glass vials before analysis onboard ship, and DON samples were stored frozen in clean plastic vials until analysis after each cruise. During three of the six expeditions (*see below*), ammonium samples were stored at in situ temperature in clean plastic vials until analysis after each cruise. Ammonium samples from the remaining three cruises were analyzed during each cruise. Samples for total dissolved carbohydrates and dissolved free monosaccharides were stored in clean glass tubes at in situ temperature for at most 12 h before analysis onboard ship.

At the Ceara Rise sediments were collected using a multiple corer operated by R. Jahnke (SkIO). Cores were sectioned at 4° under N₂. Pore waters were extracted by centrifugation and subsequently drawn into glass syringes and filtered through pre-rinsed Millipore Millex-HV filters (Martin and McCorkle 1993; Martin and Sayles 1996). Benthic in situ chamber flux measurements at the Ceara Rise site were carried out by R. Jahnke. Methods and results are discussed in Jahnke and Jahnke (2004).

Analytical methods—DOC was determined using a SHI-MADZU TOC-5000 total carbon analyzer based on the high-temperature catalytic oxidation (HTCO) technique or a home-built HTCO instrument (Martin and McCorkle 1993). Inorganic carbon species were removed by adding 50 μ L of 2 mol L⁻¹ HCl (pro analysi (PA) quality) and purging the sample for 10 min with ultrapure synthetic air, prior to the HTC oxidation. The catalyst (3% Pt on Al₂O₃ spheres) was preconditioned (300 × 50 μ L injections of MQ-water) to get a stable and low system blank (typically ~2 μ mol L⁻¹ C) before analyzing the samples. All samples were analyzed in triplicate with an analytical precision of better than 3% (pore-water samples) and 8% (benthic chamber samples) relative standard deviation

(RSD; $n = 10$). The instrument was calibrated and corrected for drift with Certified Reference Material (CRM, Prof. D. Hansell, RSMAS, University of Miami).

Determination of ammonium was performed onboard ship during the D222, M42/2, and D236 cruises (Table 1) by applying the standard photometric method either manually or by using an autoanalyzer. Replicate measurements ($n = 15$) of the standard solutions resulted in a RSD of 5–10% in the concentration range of 2–17 $\mu\text{mol L}^{-1}$. All standard solutions were diluted with artificial seawater (ASW). For the D226, D231, and Ch142 cruises the ammonium samples were analyzed after each cruise using a Bran and Luebbe TRAACS 2000 autoanalyzer.

DON concentrations were calculated as the difference between total dissolved nitrogen (TDN) and the sum of nitrate (Brunnegård et al. 2004) plus ammonium concentrations. TDN samples were oxidized with the persulfate oxidation method, as described in Bronk et al. (2000). The formed nitrate was analyzed on a TRAACS autoanalyzer (the same as for the ammonium samples). To check the oxidation yield, CRM (Deep Sargasso Sea water, reference lot No. 12-00, Prof. D. Hansell) and two different concentrations of urea and glycine were treated and run as normal samples. All other samples were compensated for the recovery obtained on these samples. The CRM concentration reported by the distributor was 21.1 $\mu\text{mol L}^{-1}$, and we obtained on average 23.0 $\mu\text{mol L}^{-1}$ in our determinations. The samples were diluted with ASW before the oxidation step and, when necessary, just prior to analysis as well. ASW was run as a blank, and its contribution to the TDN concentration (although very low) was subtracted from the diluted samples.

Total dissolved carbohydrates were determined with the MBTH method according to Pakulski and Benner (1992). Total dissolved carbohydrates detected by the MBTH method include all molecules with sugar units, which undergo hydrolysis with 12 mol L^{-1} H_2SO_4 , such as oligo- and polysaccharides as well as smaller molecules like pyruvate. Ten milliliters of the filtered pore-water or bottom-water sample was evaporated in a vacuum centrifuge (Heto). Calibration was done against glucose standard curves. Standards were stored in the dark and prepared in filtered seawater to have the same matrix in samples and standards. Blanks (as specified by Pakulski and Benner [1992]) were subtracted from each sample and standard (<7% of the absorbance). Background sugars in the standard matrix were measured and subtracted from all standard absorbances.

Dissolved free monosaccharides were determined by high-pressure anion exchange liquid chromatography–pulsed amperometric detection. This methodology shows outstanding detection limits and the ability to handle large sets of samples (e.g., Cheng and Kaplan 2001). Without further treatment, the filtered pore-water and bottom-water samples were directly placed in a Jasco 851-AS auto-sampler, which kept the samples cold and injected 50 μL into the chromatographic system. Two Jasco PU980 pumps were used. One delivered the isocratic separation mobile phase, while the other was aimed for the column reconditioning solution used between the separations. The

analytical column used was a CarboPac PA10 (4 \times 250 mm) protected by a PA10 (4 \times 50 mm) precolumn from Dionex Corporation. Mobile phase comprised 18 mmol L^{-1} NaOH in water, and the flow rate was 1 mL min^{-1} . Between every chromatogram the column was reconditioned for 10 min with 200 mmol L^{-1} NaOH, followed by 20 min of mobile phase before injection. The detector used was an ED40 from Dionex Corporation. Bottom water/pore water was injected directly and undiluted on the column in the alkaline mobile phase. This resulted in a buildup of $\text{Mg}(\text{OH})_2$ on the column top, which after approximately 50 injections gave rise to an increased back-pressure. To rinse the column, 0.5 mol L^{-1} HCl was pumped through the system for 20 min after every 50 injections. Milli-Q water was pumped through the column before and after the acid-washing treatments.

The decomposition of dissolved carbohydrates in this concentration range is very rapid, and the concentration easily decreases to half during a period of 2 d, even if samples are kept cold. Thus, we ran the samples as soon as possible and made new standard solutions every day from stock standards kept in a freezer.

Calculation of effluxes from pore-water gradients—Fluxes out of the sediment of ammonium and all dissolved organic constituents were calculated using Fick's first law of diffusion ($J_{\text{sed}} = -\phi \times D_{\text{sed}} \times dC/dz$; where ϕ is the porosity, D_{sed} is the whole-sediment molecular diffusion coefficient, and dC/dz is the concentration gradient). Porosity was obtained from Witbaard et al. (2000), who measured resistivity and calculated porosity in 41 multiple cores from PAP sediments between 1996 and 1997. The averaged profile ($n = 41$) starts at a porosity of ~ 0.90 at the surface and decreases down-core to ≤ 0.77 at 5 cm in depth, where it levels out. The diffusion coefficient in seawater (D_{sw}) for ammonium was obtained from Schulz (2000, and references therein) and was adjusted to the in situ temperature ($+2.6^\circ\text{C}$) using the Stokes–Einstein relation, giving a D_{sw} of 1.0×10^{-5} $\text{cm}^2 \text{s}^{-1}$. To calculate the D_{sed} (Eq. 1), we divided D_{sw} by the tortuosity (θ) raised to the second power, obtained by Boudreau's law, $\theta^2 = 1 - \ln(\phi^2)$:

$$D_{\text{sed}} = \frac{D_{\text{sw}}}{1 - \ln(\phi^2)} \quad (1)$$

A D_{sed} of $7.2\text{--}8.3 \times 10^{-6}$ $\text{cm}^2 \text{s}^{-1}$ was obtained for ammonium.

For ammonium and all dissolved organic constituents the concentration difference between the near-surface pore-water maximum and the bottom water ($z = 0$) was used as the gradient across the sediment–water interface (dC/dz) in the flux calculations. The pore-water maximum was always situated within the top 0–20 mm of the sediment, most often within the uppermost 0–10 mm. This means that with a 5-mm vertical resolution, the gradient was calculated from two to five concentration measurements.

Burdige and Gardner (1998) concluded, from ultrafiltration of different molecular size classes of DOC, that 60–70% of the pore-water DOC in many continental margin

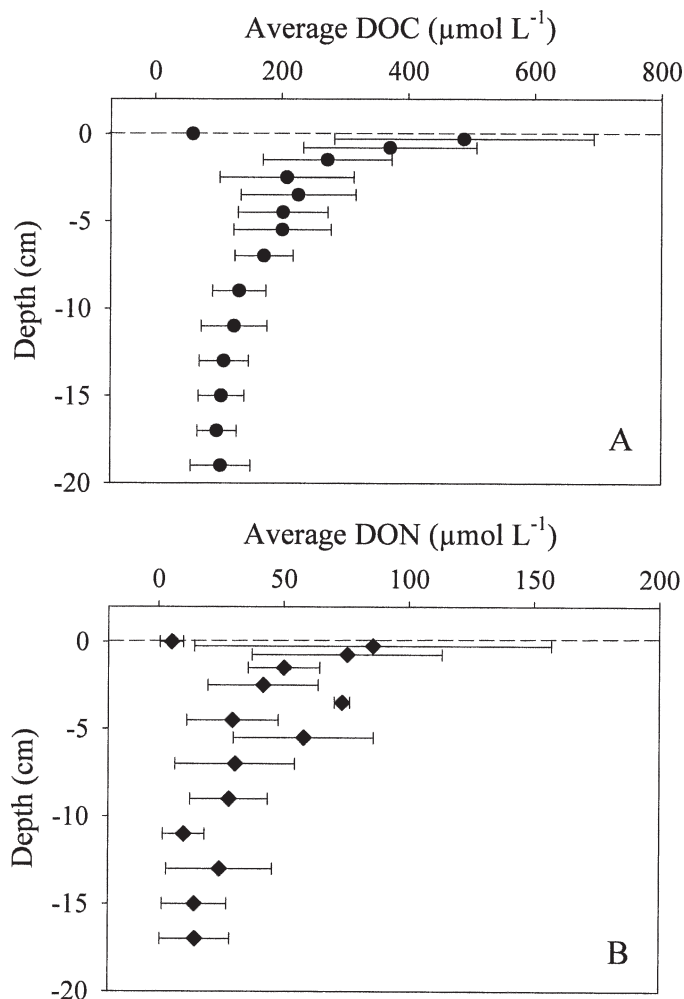


Fig. 1. Concentration of (A) DOC and (B) DON in the pore water of sediment cores collected from PAP. The average concentration in 11 (DOC) and 5 (DON) cores is given. Bottom-water concentration is indicated at depth = 0 (dashed line). Error bars denote ± 1 standard deviation (SD).

sediments has molecular weights (MW) of less than 3 kDa, and the remaining 30–40% is equally divided between the 3–100-kDa and the >100-kDa fractions. The MW of pore-water DON in estuarine sediments (Chesapeake Bay) has been reported to be mainly between 1 and 10 kDa (Burdige and Zheng 1998), and the fraction of pore-water DON with MW of less than 3 kDa has been found to decrease from $84 \pm 11\%$ in Chesapeake Bay to $62 \pm 18\%$ at the Mid-Atlantic shelf/slope break (D. Burdige unpubl. data). These results indicate that the average MW of pore-water DOC and DON in continental margin sediments are rather similar. Benner (2002) stated that in deep ocean water (>1,000 m) 75–80% of the DOC is found as low-MW DOC (≤ 1 kDa). However, the MW of dissolved organic matter (DOM) in abyssal sediment pore water is not known, but Benner's results indicate that it should be lower than in continental margin sediments, and the results of Burdige and co-workers indicate that the DOM fraction with a MW less than 3 kDa decreases from shallow to deeper environments. Based on the above, we assumed that all our

dissolved organic pore-water constituents (other than the dissolved free monosaccharides) had the same MW composition, that the pore-water DOM was composed of two fractions having fixed MW of 700 Da and 5 kDa, and that a 50%/50% mixture of these was present in the pore water. By using the empirical relationship between diffusion coefficient and MW given by Burdige et al. (1992),

$$\log D^0 = 1.72 - 0.39 \times \log MW \quad (2)$$

a D_{sw} of $3.0 \times 10^{-6} \text{ cm}^2 \text{ s}^{-1}$ at 25°C was calculated. The D_{sw} was then adjusted to the in situ temperature using the Stokes–Einstein relation ($1.5 \times 10^{-6} \text{ cm}^2 \text{ s}^{-1}$). A D_{sed} of $1.1\text{--}1.3 \times 10^{-6} \text{ cm}^2 \text{ s}^{-1}$ was obtained (Eq. 1) depending on the position of the DOM pore-water maximum.

Results

All dissolved organic constituents and ammonium displayed a distinct near-surface pore-water maximum within the top 0–20 mm of the sediment, most often within the uppermost 0–10 mm. This was observed in late winter, spring, summer, and early fall (i.e., regardless of season) and during all cruises. The variation of surface-water temperature between the cruises ranged from $\sim 11^\circ\text{C}$ (late winter) to $\sim 18^\circ\text{C}$ (late summer), whereas the bottom-water temperature was constant at $\sim 2.6^\circ\text{C}$.

Pore-water DOC concentrations at PAP (Figs. 1A, 2) were elevated over bottom-water values ($50\text{--}60 \mu\text{mol L}^{-1}$) up to an order of magnitude in the surficial sediment. DOC profiles in 11 different cores all showed a sharp near-surface maximum of on average about $500 \mu\text{mol L}^{-1}$ in the top 0–10 mm of the sediment, decreasing to $100\text{--}200 \mu\text{mol L}^{-1}$ at 6–7 cm in depth and finally asymptotically reaching a stable concentration of $\sim 100 \mu\text{mol L}^{-1}$ below this depth. The variability of DOC concentration between the cores was larger in the near-surface maximum than below it (Fig. 1A). The average diffusive DOC efflux calculated from these near-surface gradients was $1.4 \pm 0.89 \text{ mmol C m}^{-2} \text{ d}^{-1}$ ($n = 11$ during four cruises; Table 2).

The pore-water DOC distributions at the other Atlantic deep-sea site at the base of the Ceara Rise was very similar to those at PAP, with clear near-surface maxima (Fig. 2). At this site, direct in situ measurements of DOC fluxes were simultaneously made with benthic chambers. The flux calculated from the pore-water/bottom-water DOC gradient was markedly larger than that estimated at the same locality and at the same time with chambers (Fig. 3).

DON displayed a pore-water distribution at PAP (Fig. 1B) similar to that of DOC. The bottom-water concentration of $5.2 \pm 4.6 \mu\text{mol L}^{-1}$ was elevated to typically $80\text{--}90 \mu\text{mol L}^{-1}$ in the near-surface maximum, below which it decreased and approached a concentration of on average about $14 \mu\text{mol L}^{-1}$ at depth. The average diffusive DON efflux calculated from these near-surface gradients was $0.22 \pm 0.31 \text{ mmol N m}^{-2} \text{ d}^{-1}$ ($n = 5$ during four cruises; Table 2). The C:N ratio of pore-water DOM was about 5.7 in the near-surface maximum and about 7.2 below 12 cm in depth.

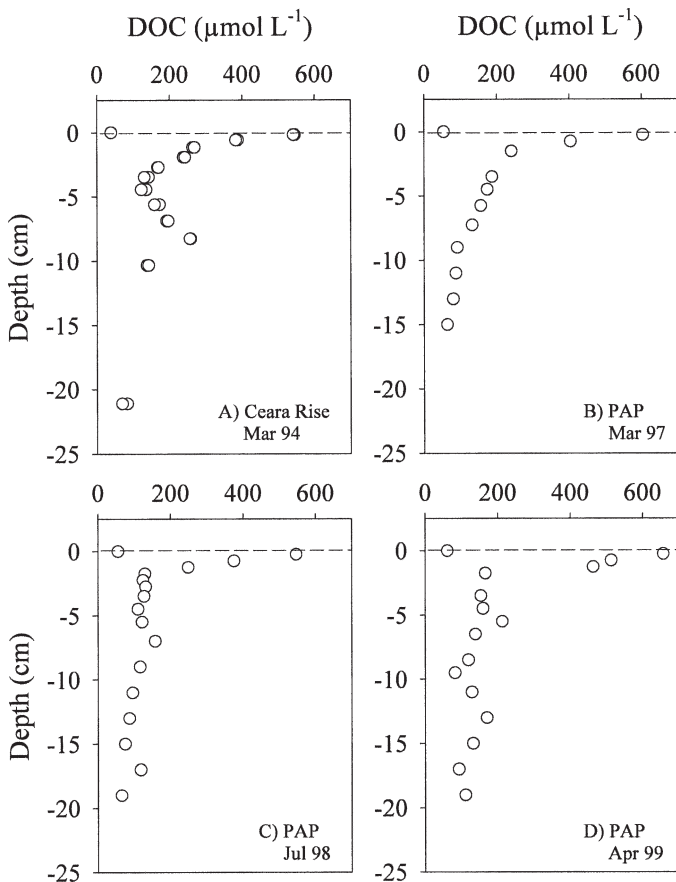


Fig. 2. (A–D) Examples of DOC distributions in pore waters of individual cores recovered from the Ceara Rise (depth, 4,675 m) and from PAP (depth, 4,800–4,847 m). Date of core collection is indicated. Bottom-water concentration is indicated at depth = 0 (dashed line).

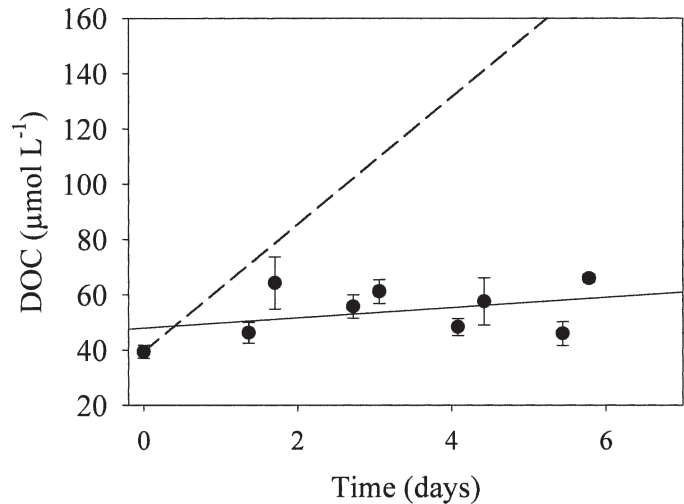


Fig. 3. Evolution of DOC concentration with time in a flux chamber deployed in situ at the Ceara Rise (depth, 4,675 m) in March 1994 (circles). Error bars denote ± 1 standard deviation (SD) of replicate analyses. The solid line is a linear regression of all chamber data points corresponding to a DOC flux of $0.18 \text{ mmol C m}^{-2} \text{ d}^{-1}$ (assuming a chamber overlying water height of 10 cm). The dashed line is hypothetical and denotes the DOC concentration that would have been measured in the chamber with the DOC flux predicted from the surficial pore-water gradient ($2.3 \text{ mmol C m}^{-2} \text{ d}^{-1}$) in a core recovered from the Ceara Rise at the same time (Fig. 2).

The type of near-surface pore-water ammonium maxima, which previously have been observed in other deep-sea sediments in recovered cores, were also found at PAP (Fig. 4). Concentrations in the maxima were typically $12\text{--}17 \mu\text{mol L}^{-1}$, whereas the bottom-water concentration normally was $<1 \mu\text{mol L}^{-1}$. Below the maxima ammonium

Table 2. Diffusive effluxes ($\mu\text{mol C or N m}^{-2} \text{ d}^{-1}$) calculated from near-surface pore water gradients in sediment cores recovered from the PAP.*

Cruise ID	Date	DOC	DON	NH ₄	Tot diss carb	Monosacc†
D222	Aug 1996			7		
D226	Mar 1997	2,360		5	304	23
D226	Mar 1997	1,930		10	255	86
D226	Mar 1997	2,120		3	119	73
D226	Mar 1997	1,920		0.2	314	66
D231	Mar 1998	310		25; 150		
D231	Mar 1998		23	28; 25		
D231	Mar 1998		65	119; 183; 46		
M42/2	Aug 1998	695		181		
M42/2	Aug 1998	129				
M42/2	Aug 1998	1,890				
M42/2	Aug 1998	2,380	775			
M42/2	Aug 1998	1,130		10		
D236	Aug 1998			174		
D236	Sep 1998		142			
Ch142	May 1999	230				
Ch142	May 1999		103	105		
Average \pm SD		1,370 \pm 890	221 \pm 312	67 \pm 72	248 \pm 90	62 \pm 27

* DOC, dissolved organic carbon; DON, dissolved organic nitrogen; Tot diss carb, total dissolved carbohydrates; SD, standard deviation.

† Monosacc, dissolved free monosaccharides. Flux of the sum of the eight to nine quantified free dissolved monosaccharides in each core is given. A D_{sw} at $+2.6^\circ\text{C}$ of $2.9 \times 10^{-6} \text{ cm}^2 \text{ s}^{-1}$ was used.

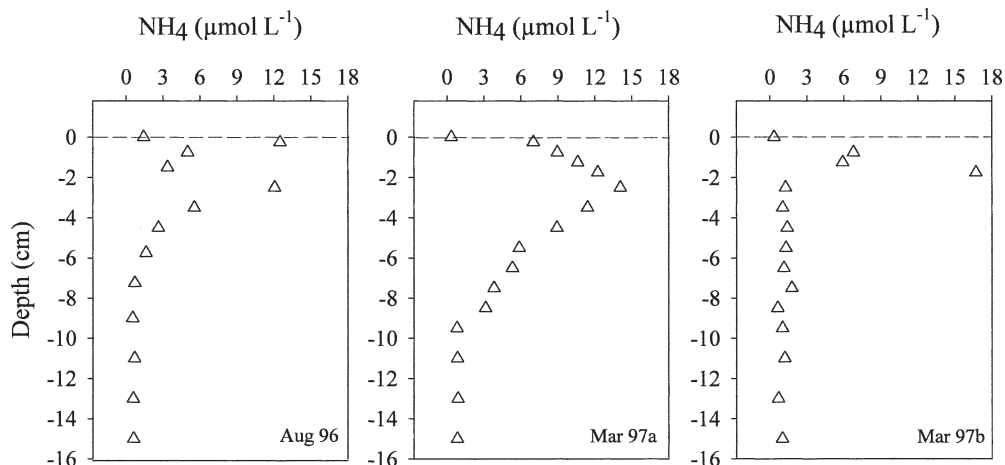


Fig. 4. Examples of pore-water NH_4 distributions in cores recovered from PAP. Date of core collection is indicated. Two cores for NH_4 were collected in March 1997. Bottom-water concentration is indicated at depth = 0 (dashed line).

decreased and approached a concentration of about $1 \mu\text{mol L}^{-1}$ at depth in the cores. The average diffusive ammonium efflux calculated from these near-surface gradients was $67 \pm 72 \mu\text{mol N m}^{-2} \text{d}^{-1}$ ($n = 16$ during six cruises; Table 2).

The average pore-water concentration of total dissolved carbohydrates at PAP (Fig. 5A) was about $60 \mu\text{mol L}^{-1}$ (in terms of C) in the top 0–5 mm of the sediment, which is more than an order of magnitude higher than in the bottom water ($4 \mu\text{mol L}^{-1}$ in the water overlying the collected MUC cores and below $1 \mu\text{mol L}^{-1}$ C in the Rosette samples). From the near-surface maximum the concentrations decreased and approached a concentration of about $10 \mu\text{mol L}^{-1}$ C at 15 cm in depth. The fraction of DOC being made up of total dissolved carbohydrates was enhanced from <2% in the bottom water to on average 13–15% in the near-surface pore-water peak. The average diffusive efflux of total dissolved carbohydrates calculated from these near-surface gradients was $0.25 \pm 0.09 \text{ mmol C m}^{-2} \text{d}^{-1}$ ($n = 4$ during one cruise; Table 2), which was 18% of the DOC flux.

The individual dissolved free monosaccharides quantified in PAP pore waters were inositol, mannitol, fucose, arabinose, galactose, glucose, mannose, fructose, and ribose. Sorbose and galactosamine were not detected. The most abundant saccharides in the near-surface pore-water maximum of most cores were mannitol and ribose, followed by arabinose, mannose, glucose, and fructose. As the column efficiency is more limited with liquid chromatography compared to gas chromatography, co-eluting saccharides cannot be avoided with this method. The following saccharides gave the same retention time: rhamnose/mannose, xylose/glucoseamine/arabinose, and deoxyribose/fucose. These have been quantified as mannose, arabinose, and fucose, respectively, as these three have been reported to be the most abundant monosaccharides in seawater (e.g., Sakugawa and Handa 1983). Inositol was detected in approximately 50% of all samples, but because of its poor retention on the column it was probably often obscured by the front peak.

The concentration of the sum of the nine quantified dissolved free monosaccharides in the pore water (Fig. 5B) was on average about $8 \mu\text{mol L}^{-1}$ C in the near-surface maximum at 0–5 mm in depth. The average diffusive efflux of the sum of dissolved free monosaccharides calculated from these near-surface gradients was $62 \pm 27 \mu\text{mol C m}^{-2} \text{d}^{-1}$ ($n = 4$ during one cruise; Table 2). The variability of the sum concentration of dissolved free monosaccharides between the cores was larger in the near-surface maximum than below it. Below the maximum the concentration decreased exponentially with depth, with a factor of 2 for every 3 cm, to a background concentration of about $1 \mu\text{mol L}^{-1}$. The attenuation with depth of the free monosaccharide concentration below the maximum clearly was faster than that of total carbohydrates (Fig. 5A,B). Within the maximum the sum of free monosaccharides made up on average 13–16% of total carbohydrates, whereas the contribution was 7–9% below 10 cm in depth. An example of the pore-water distribution of individual dissolved free monosaccharides is given in Fig. 5C.

Discussion

It is well known that the biomass of bacteria and small size-class fauna is highest at and near the surface of deep-sea sediments and that it declines rapidly with depth into deposits. This distribution pattern has also been found at PAP and other Northeast Atlantic localities (e.g., Pfannkuche and Soltwedel 1998; Eardly et al. 2001). Thus, it is to be expected that dissolved organic substances and other microbial metabolites are distributed accordingly. However, it is also reasonable to expect that if cells become leaky during sediment recovery, then the concentration of these substances would be greatly enhanced at and near the sediment–water interface. In addition, exoenzymatic hydrolytic activity would be expected to be stimulated above natural levels by the enhanced availability of this fresh material, and the depth distribution of this stimulated activity should be in accordance with that of the fresh

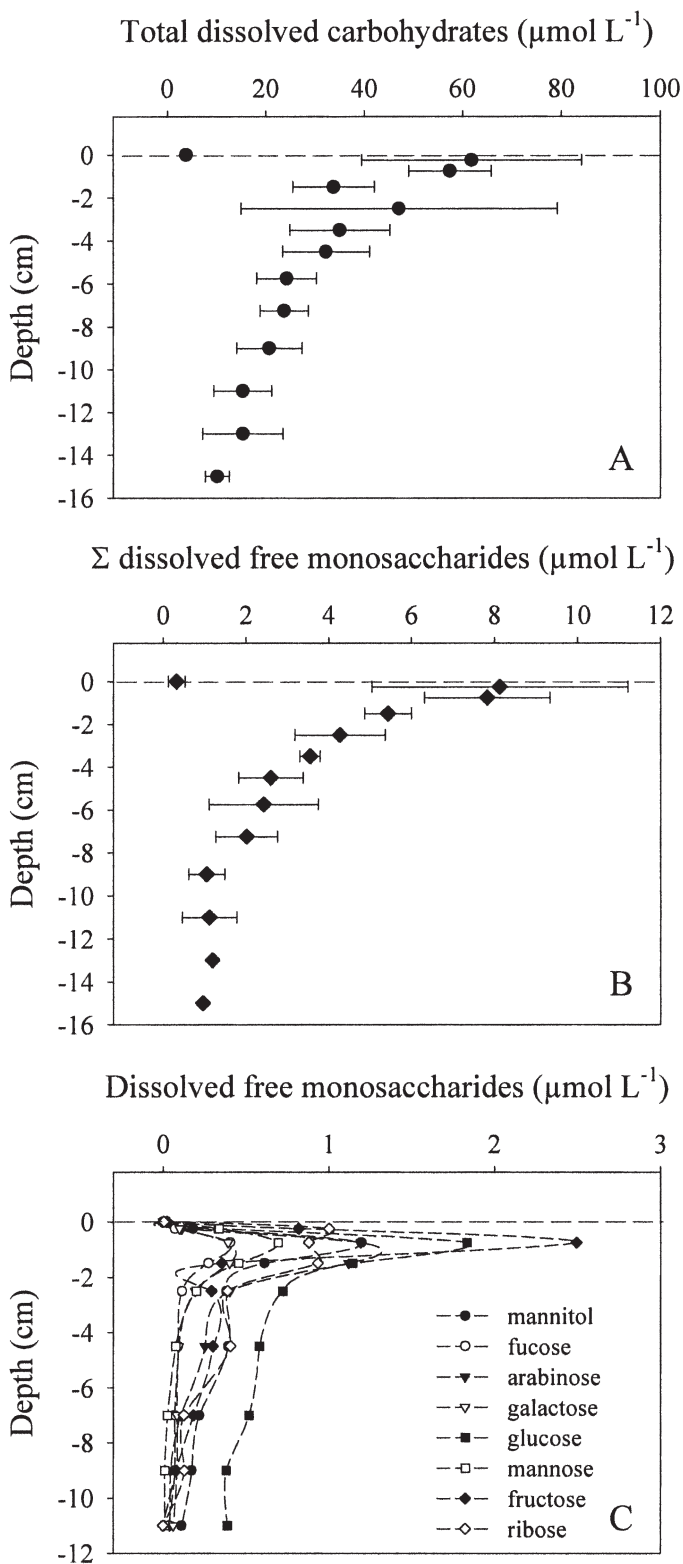


Fig. 5. (A) Total dissolved carbohydrate concentration; (B) sum concentration of dissolved free monosaccharides; and (C) example of distributions of individual dissolved free monosaccharides in the pore water of PAP sediments. Concentrations are given as $\mu\text{mol C L}^{-1}$. In panels A and B, the average concentration of four cores is given, and in each of these cores, the Σ free

material and hence of biomass. Below we present several pieces of evidence and arguments in favor of the theory that near-surface maxima of pore-water organic solutes in recovered abyssal sediment are predominantly induced by an artifact and do not exist in situ.

Near-surface maxima—Real or artificial?—Organic carbon oxidation (C_{ox}) rates in PAP sediments were measured in situ with chamber landers on these cruises. The average C_{ox} rate (DIC effluxes corrected for CaCO_3 dissolution) during 1996–1999 was $0.46 \pm 0.37 \text{ mmol C m}^{-2} \text{ d}^{-1}$ ($n = 31$, four cruises) (Ståhl et al. 2004b). The DOC efflux from PAP sediments (on average $1.4 \pm 0.89 \text{ mmol C m}^{-2} \text{ d}^{-1}$ during the same time period) would thus be about 300% of C_{ox} rates if the near-surface pore-water DOC gradients reflected in situ conditions. It would be unexpected if the benthic community allowed such a large amount of labile carbon to be lost to the overlying water.

An average POC input to the sediment could be estimated as the sum of C_{ox} rates, organic carbon burial rates (on average $0.03 \pm 0.01 \text{ mmol C m}^{-2} \text{ d}^{-1}$) (Ståhl et al. 2004b), and calculated DOC effluxes. This POC input during 1996–1999 ($1.86 \pm 0.83 \text{ mmol C m}^{-2} \text{ d}^{-1}$) was almost eight times higher than the mean annually integrated POC rain rate of $0.24 \pm 0.06 \text{ mmol C m}^{-2} \text{ d}^{-1}$ measured during 1997–1999 at PAP with sediment traps at 3,000 m in depth (Lampitt et al. 2001). For the period 1989–1999, Lampitt et al. reported a mean annually integrated POC rain rate of $0.27 \pm 0.13 \text{ mmol C m}^{-2} \text{ d}^{-1}$. It is widely agreed that sediment traps often underestimate vertical particle fluxes, but the traps at 3,000 m (1,800 m above bottom) were calibrated, had trapping efficiencies of up to 95%, and it was thought that the sediment trap data from 3,000 m provided the best estimate of primary downward flux in the region (Lampitt et al. 2001). Without a DOC efflux, the benthic demand for POC and the POC supply from overlying water were not significantly different (Ståhl et al. 2004b).

DOC fluxes were measured in situ with benthic chambers at the Ceara Rise (water depth, 4,675 m) in the Atlantic in parallel with pore-water DOC measurements in recovered cores. Although there was some uncertainty about the magnitude of the flux in the chambers, there is no doubt that the flux predicted from near-surface pore-water gradients in surface processed cores ($2.3 \text{ mmol C m}^{-2} \text{ d}^{-1}$) was much larger (>12 times) than the flux that could be estimated in the chamber ($0.18 \text{ mmol C m}^{-2} \text{ d}^{-1}$) using linear regression of all chamber data points (Fig. 3). This comparison provides very strong evidence that the near-surface pore-water DOC maximum did not exist in situ.

The pore-water DOC gradients at PAP indicated that about 75% of the degraded POC left the sediments as DOC. Since the mean age of deep-water DOC is

←

monosaccharide concentration was calculated from the eight to nine quantified individual monosaccharides. Bottom-water concentration (water overlying MUC cores) is indicated at depth = 0 (dashed line). Error bars denote ± 1 standard deviation (SD).

approximately 6,000 yr, the DOC leaving the sediments must be relatively quickly oxidized within the deep-water column. If there was significant buildup of this DOC, the mean age would be younger. No significant DOC buildup has been directly observed; on the contrary, a 29% reduction in deep-water concentration from the northern North Atlantic to the northern North Pacific has been measured (Hansell and Carlson 1998). Thus, adding this DOC flux to the sedimentary C_{ox} rate would approximately quadruple the required deep-ocean biological oxygen demand. To be consistent with observed oxygen levels in the deep ocean, these results would imply that reported C_{ox} rates in deep-sea sediments are too large by a factor of 4, ^{14}C -AOU (apparent oxygen utilization) relationships underestimate oxygen consumption by a factor of 4, or the ventilation rate of the deep ocean must be four times that of current estimates (*see* Jahnke 1996, and references therein). Each of these implications seems highly unlikely, which again indicates that the pore-water gradients in recovered cores severely overestimated in situ DOC fluxes.

Vertical particulate carbohydrate fluxes were measured with sediment traps at PAP in parallel to our studies (Fabiano et al. 2001). The average diffusive efflux of total dissolved carbohydrates from the sediment in March 1997 ($0.25 \pm 0.09 \text{ mmol C m}^{-2} \text{ d}^{-1}$) was more than eight times larger than the sediment trap fluxes at 3,000 m in depth measured during the same month (about $30 \mu\text{mol C m}^{-2} \text{ d}^{-1}$). For the period ranging from September 1996 to September 1998, the average sediment trap carbohydrate flux was about $70 \mu\text{mol C m}^{-2} \text{ d}^{-1}$, which is almost four times lower than our diffusive flux estimates. With calibrated sediment traps, such large discrepancies are hard to explain by means other than artificial pore-water distributions of total dissolved carbohydrates, unless the sedimentary carbohydrate pool drastically declined with time. However, Fabiano et al. (2001) found no such trend of the carbohydrate content in the sediment between 1996 and 1998.

A PON input to PAP sediment was calculated based on in situ measured effluxes of NH_4 and NO_3 , estimated denitrification, and burial rates (Brunnegård et al. 2004) together with the diffusive effluxes of DON. The obtained average PON input during 1996–1999 of $0.29 \pm 0.31 \text{ mmol N m}^{-2} \text{ d}^{-1}$ is about 12 times larger than the mean annually integrated PON rain rate of $24 \pm 8.2 \mu\text{mol N m}^{-2} \text{ d}^{-1}$ measured at PAP with calibrated sediment traps at 3,000 m during 1997–1999 (Lampitt et al. 2001). The mean annual PON rain rate estimated for 1989–1999 from data of Lampitt et al. was $36 \pm 21 \mu\text{mol m}^{-2} \text{ d}^{-1}$. With only a small DON efflux, the benthic demand and the supply of PON are not significantly different (Brunnegård et al. 2004).

The fluxes of ammonium calculated from pore-water gradients at PAP in this study ($67 \pm 72 \mu\text{mol N m}^{-2} \text{ d}^{-1}$) were on average nine times higher than those measured simultaneously in situ at the same locality using benthic chambers ($7.5 \pm 19 \mu\text{mol m}^{-2} \text{ d}^{-1}$) (Brunnegård et al. 2004). Berelson et al. (1990) used the same approach to argue that pore-water NH_4 distributions obtained on-deck in cores from the deep Pacific were affected by artifacts.

What causes these artifacts?—It may be argued that squeezing of animals during centrifugation of sediment might have caused the near-surface pore-water DOM and ammonium maxima. In previous studies of continental margin sediments of the Skagerrak, with much higher abundance and biomass of macro- and meiofauna than were observed at PAP (De Bovee et al. 1996; Rosenberg et al. 1996), the same extraction technique with sectioning and gentle centrifugation (2,000 rpm [$670 \times g$], 30 min) was used without observing any near-surface pore-water maxima of DOC (Ståhl et al. 2004c), DON, and ammonium (Brunnegård et al. unpubl. data). The same centrifugation method was used with shelf sediments of the northern Aegean Sea, and no near-surface pore-water DOC maxima were found (Ståhl et al. 2004a). Martin and McCorkle (1993) showed that centrifugation might cause artificially high DOC pore-water concentrations when faunal biomass is high. However, faunal biomass is low in PAP and Ceara Rise sediments. Another very thorough continental margin study on this subject is that of Holcombe et al. (2001). They convincingly showed that DOC fluxes calculated from pore-water gradients obtained from centrifugation as well as from in situ dialysis peepers were of similar magnitude as DOC fluxes obtained from in situ chamber measurements and from whole-core incubations. We conclude that it is highly unlikely that sectioning/centrifugation produced the near-surface pore-water DOM and ammonium maxima observed in this study.

The expansion of water as a result of decompression when bringing sediment cores from the abyssal seafloor to the surface has been given as a partial explanation for shallower penetration and steeper gradients of oxygen in surface processed cores than in situ (Glud et al. 1994). In contrast to oxygen, DOM is produced (net) in sediments with bottom-water concentrations lower than those in the pore water. If the pore-water DOM maxima existed in situ, pore-water expansion due to decompression would make them disappear or would at least render them less pronounced. However, expansion of water during decompression from 480 to 1 bar, which is about 2.4% (Kell 1975), can have negative effects on cell viability and membrane function (*see below*). Expansion of water as a result of warming is only 0.13% from 2.6°C to 18°C (Kell 1975) and can in this context be neglected in comparison with decompression-induced expansion.

Hydrostatic pressure and temperature also influence gas solubility. Is it likely that gas bubbles are created as a result of decompression (480 to 1 bar) and temperature elevation (2.6°C to 11°C [late winter] and 18°C [summer])? Oxygen can be neglected in this context since its bottom-water concentration at PAP ($251 \pm 2.27 \mu\text{mol L}^{-1}$ was obtained in this study) and its solubility at the surface ($240 \mu\text{mol L}^{-1}$ at 18°C and salinity 35) are similar. Since deep-sea water was saturated with N_2 when it left contact with the atmosphere, and if we neglect the production of N_2 through denitrification in the water column and deep-sea sediments of the Atlantic, decompression should be of minor importance. However, since deep-water formation takes place in the northern North Atlantic, where surface-water temperature is low (around 0°C) and where the surface water is saturated

with N₂ at this low temperature before sinking, warming this water up to 18°C (at constant salinity) leads to a N₂ saturation of at least 144% (Weiss 1970). This most likely implies creation of N₂ bubbles since there are a great number of condensation nuclei at the surface of a sediment core and within organisms. Changing the prevailing conditions at the seafloor of PAP to those at the surface in summer, and taking into account precipitation of CaCO₃ in surficial sediment (total alkalinity ~2,200 μmol L⁻¹, DIC ~2,000 μmol L⁻¹), will lead to a partial pressure of CO₂ (pCO₂) of around 500 μatm. This is about 135% of atmospheric equilibrium level, which makes gas bubble formation even more likely, and bubbles are thus plausibly created as a result of supersaturation of both N₂ and CO₂. Formation of gas bubbles within cells could make them burst or could induce leakage.

We have presented evidence that the observed pore-water maxima are induced by an artifact and are not related to centrifugation of sediment. The combined effect of decompression and warming has previously been shown to inactivate and even kill piezophilic and psychophilic bacteria and meiofauna in deep-sea sediments (Smith and Hinga 1983; Turley et al. 1988). Bacterial cells—including those without gas vacuoles—from deep-sea sediments have been found to be damaged, to rupture, and/or to undergo lysis when decompressed to atmospheric pressure (Yayanos and Dietz 1983; Chastain and Yayanos 1991; Yayanos 2001; Bartlett 2002; Park and Clark 2002). Disturbance, rupture, or bursting of bacterial biomass, directly or indirectly caused by decompression and/or warming, is thus the most likely explanation for the formation of the DOM pore-water maxima observed in this study, and which have been reported to reflect in situ conditions in previous studies.

The attenuation of the sum-concentration of dissolved free monosaccharides with depth below the pore-water maximum was faster than that of total dissolved carbohydrates (Fig. 5A,B), which indicates that the source near the sediment–water interface was relatively more dominant for free monosaccharides than for carbohydrates in general. Since leakage from cells should enhance concentration above background for monosaccharides to a larger extent than for total carbohydrates, this observation is consistent with bursting or leaky cells within the top 0–5 mm of the sediment being the main source for dissolved free monosaccharides.

The average C:N ratio of pore-water DOM within the near-surface maxima was about 5.7. Below 10 cm in sediment depth, where DOC and DON concentrations had leveled out, the average C:N ratio was about 7.2 (Fig. 1), indicating that the DOM within the maximum was more nitrogen rich than it was below the maximum. This provides additional evidence in support of the idea that the maxima is caused by lysis of or leakage from cells.

The monosaccharide composition of the pore water was determined in this study, and we found that most often, ribose and mannitol were the most abundant dissolved free monosaccharides within the pore-water maxima. Abundance and relative contribution of individual

monosaccharides have been used to identify material sources in aquatic environments, and ribose and mannose have been found to be common among those indicative of bacteria (Moers et al. 1989, 1990). Mannitol is the reduced form of mannose and probably a bacterial metabolite of the latter. Our observation may thus indicate that lysis of or leakage from predominantly bacterial cells created the monosaccharide maxima.

Studies of abyssal sediments in the Northeast Atlantic (Pfannkuche 1993; Thiel and Rice 1995; Heip et al. 2001) have shown that faunal densities are low and that the living sediment biomass is made up mainly of bacteria (≥90%). At the nearby BIOTRANS station, west of PAP, a bacterial biomass of 7–20 μg C mL⁻¹ in surficial sediment was found (Thiel et al. 1988/89). Using a conservative bacterial biomass estimate of 10 μg C mL⁻¹, a porosity of 0.85, and assuming that 50% of the bacterial cell C content is released to the pore water in dissolved form upon core recovery, the DOC concentration would be enhanced with about 500 μmol L⁻¹ above background. With most of the bacteria bursting and releasing organic carbon in dissolved form to the pore water, this DOC injection would produce a concentration, which is very close to what we measured in the near-surface maxima. With the reasoning above, but by using an estimated bacterial biomass in PAP sediment of 0.25 g C m⁻² (Witte et al. 2003) and with 75% of this biomass existing in the uppermost 2 cm of the sediment, a very similar DOC injection is obtained. We conclude that the organic carbon content of bacterial biomass in Northeast Atlantic abyssal sediments can produce the observed near-surface maxima.

Implications and recommendations—Previous estimates of microbial biomass in abyssal sediments may be underestimated as a result of the likely difficulty inherent in counting bacterial cells that have lysed or the cell envelopes of which have ruptured.

In order to avoid overestimates, measurements of DOC, DON, total dissolved carbohydrates, dissolved free monosaccharides, and presumably other specific dissolved organic compounds in pore water of abyssal sediments should be made in situ or in undecompressed sediment cores, which have not experienced temperature elevation. Another alternative to avoid recovery artifacts is to separate the pore water from the sediment in situ before analyzing the pore water onboard ship. This can be accomplished using equilibration probes, such as peepers and diffusion equilibration in thin films.

Hydrolytic exoenzymatic activity in deep-sea sediments has been found to be highest at the sediment–water interface and to decline rapidly with depth into deposits (e.g., Boetius et al. 2000). Since exoenzymes are inducible, their activities in surficial sediments will be stimulated above natural levels by the availability of fresh organic matter released from lysed or leaky microbial cells. Measurements of exoenzymatic activity in abyssal sediments should thus be made in situ or in undecompressed sediment cores, which have not been warmed up, to avoid overestimates. This has rarely been done previously.

We cannot rule out the possibility that the core recovery artifacts of the type we consistently observed are restricted to sediments at water depths greater than a certain threshold. If such a threshold exists, then the depth of this threshold should be influenced by the magnitude and, plausibly, the composition of the biomass present, which in turn is a function of the rate of organic matter deposition to the sediment. Since only the upper few hundred meters of the water column are relatively warm, the existence of a depth threshold should indicate that decompression is the main factor creating the artifacts. However, our calculations showed that temperature elevation during core recovery from the abyss gives a N₂ saturation of about 150%, and the combined effect of warming and decompression yields a CO₂ saturation of about 135%, which, plausibly, is associated with bubble formation creating cell bursting. We have to await further studies to confirm or rule out the existence of such a pressure threshold and to better constrain the relative importance of decompression versus temperature elevation in creating the core recovery artifacts. Future studies may also show whether the influence of decompression and temperature elevation on physical-chemical parameters, such as gas solubility and water expansion, or *directly* on biological parameters, such as cell viability and membrane function, (or if the second effect is a result of the first) provides a more complete mechanistic explanation for the observed artifacts.

References

- ALLER, R. C., P. O. J. HALL, P. D. RUDE, AND J. Y. ALLER. 1998. Biogeochemical heterogeneity and suboxic diagenesis in hemipelagic sediments of the Panama Basin. *Deep-Sea Res. Part I Oceanogr. Res. Pap.* **45**: 133–165.
- BARTLETT, D. H. 2002. Pressure effects on in vivo microbial processes. *Biochim. Biophys. Acta* **1595**: 367–381.
- BENNER, R. 2002. Chemical composition and reactivity, p. 59–90. *In* D. A. Hansell and C. A. Carlson [eds.], *Biogeochemistry of marine dissolved organic matter*. Academic Press.
- BERELSON, W. M., D. E. HAMMOND, D. O'NEIL, X.-M. XU, C. CHIN, AND J. ZUKIN. 1990. Benthic fluxes and pore water studies in sediments from the central equatorial north Pacific: Nutrient diagenesis. *Geochim. Cosmochim. Acta* **50**: 3001–3013.
- BILLETT, D. S. M., R. S. LAMPITT, A. L. RICE, AND R. F. C. MANTOURA. 1983. Seasonal sedimentation of phytoplankton to the deep-sea benthos. *Nature (Lond.)* **302**: 520–522.
- BOETIUS, A., T. FERDELMAN, AND K. LOCHTE. 2000. Bacterial activity in sediments of the deep Arabian Sea in relation to vertical flux. *Deep-Sea Res. II* **47**: 2835–2875.
- BRONK, D. A., M. W. LOMAS, P. M. GLIBERT, K. J. SCHUKERT, AND M. P. SANDERSON. 2000. Total dissolved nitrogen analysis: Comparisons between the persulfate, UV and high temperature oxidation methods. *Mar. Chem.* **69**: 163–178.
- BRUNNEGÅRD, J., S. GRANDEL, H. STÅHL, A. TENGBERG, AND P. O. J. HALL. 2004. Nitrogen cycling in deep-sea sediments of the Porcupine Abyssal Plain, NE Atlantic. *Prog. Oceanogr.* **63**: 159–181.
- BURDIGE, D. J., M. J. ALPERIN, J. HOMSTEAD, AND C. S. MARTENS. 1992. The role of benthic fluxes of dissolved organic-carbon in oceanic and sedimentary carbon cycling. *Geophys. Res. Lett.* **19**: 1851–1854.
- , W. M. BERELSON, K. H. COALE, J. MCMANUS, AND K. S. JOHNSON. 1999. Fluxes of dissolved organic carbon from California continental margin sediments. *Geochim. Cosmochim. Acta* **63**: 1507–1515.
- , AND K. G. GARDNER. 1998. Molecular weight distribution of dissolved organic carbon in marine sediment pore waters. *Mar. Chem.* **62**: 45–64.
- , AND S. ZHENG. 1998. The biogeochemical cycling of dissolved organic nitrogen in estuarine sediments. *Limnol. Oceanogr.* **43**: 1796–1813.
- CHASTAIN, R. A., AND A. A. YAYANOS. 1991. Ultrastructural changes in an obligately barophilic marine bacterium after decompression. *Appl. Environ. Microbiol.* **57**: 1489–1497.
- CHENG, X. H., AND L. A. KAPLAN. 2001. Improved analysis of dissolved carbohydrates in stream water with HPLC-PAD. *Anal. Chem.* **73**: 458–461.
- DE BOVEE, F., P. O. J. HALL, S. HULTH, G. HULTHE, A. LANDEN, AND A. TENGBERG. 1996. Quantitative distribution of metazoan meiofauna in continental margin sediments of the Skagerrak (northeastern North Sea). *J. Sea Res.* **35**: 189–197.
- DEMING, J. W., AND P. L. YAGER. 1992. Natural bacterial assemblages in deep-sea sediments: Towards a global view, p. 11–27. *In* G. T. Rowe and V. Pariente [eds.], *Deep-sea food chains and the global carbon cycle*. NATO-ASI Series C, Mathematical and Physical Sciences. Kluwer.
- EARDLY, D. F., M. W. CARTON, J. M. GALLAGHER, AND J. W. PATCHING. 2001. Bacterial abundance and activity in deep-sea sediments from the eastern North Atlantic. *Prog. Oceanogr.* **50**: 245–259.
- EPPING, E., C. VAN DER ZEE, K. SOETAERT, AND W. HELDER. 2002. On the oxidation and burial of organic carbon in sediments of the Iberian margin and Nazare Canyon (NE Atlantic). *Prog. Oceanogr.* **52**: 399–431.
- FABIANO, M., AND OTHERS. 2001. Fluxes of phytopigments and labile organic matter to the deep ocean in the NE Atlantic Ocean. *Prog. Oceanogr.* **50**: 89–104.
- FANNING, K. A., AND M. E. Q. PILSON. 1971. Interstitial silica and pH in marine sediments: Some effects of sampling procedures. *Science* **173**: 1228–1231.
- GLUD, R. N., J. K. GUNDERSEN, AND O. HOLBY. 1999. Benthic in-situ respiration in the upwelling area off central Chile. *Mar. Ecol. Prog. Ser.* **186**: 9–18.
- , B. B. JOERGENSEN, N. P. REVSBECH, AND H. D. SCHULZ. 1994. Diffusive and total oxygen uptake of deep-sea sediments in the eastern South Atlantic Ocean: In situ and laboratory measurements. *Deep-Sea Res. I* **41**: 1767–1788.
- HAMMOND, D. E., J. MCMANUS, W. M. BERELSON, T. E. KILGORE, AND R. H. POPE. 1996. Early diagenesis of organic material in equatorial Pacific sediments: Stoichiometry and kinetics. *Deep-Sea Res. II* **43**: 1365–1412.
- HANSELL, D. A., AND C. A. CARLSON. 1998. Deep-ocean gradients in the concentration of dissolved organic carbon. *Nature* **395**: 263–266.
- HEGGIE, D., C. MARIS, A. HUDSON, J. DYMOND, R. BEACH, AND J. CULLEN. 1987. Organic carbon oxidation and preservation in NW Atlantic continental margin sediments, p. 215–236. *In* P. E. Weaver and J. Thomson [eds.], *Geology and geochemistry of abyssal plains*. Geological Society of America Special Publications.
- HEIP, C. H. R., AND OTHERS. 2001. The role of the benthic biota in sedimentary metabolism and sediment-water exchange processes in the Goban Spur area (NE Atlantic). *Deep-Sea Res. Part II Top. Stud. Oceanogr.* **48**: 3223–3243.

- HOLCOMBE, B. L., R. G. KEIL, AND A. H. DEVL. 2001. Determination of pore-water dissolved organic carbon fluxes from Mexican margin sediments. *Limnol. Oceanogr.* **46**: 298–308.
- HULTH, S., A. TENGBERG, A. LANDEN, AND P. O. J. HALL. 1997. Mineralization and burial of organic carbon in sediments of the southern Weddell Sea (Antarctica). *Deep-Sea Res. Part I Oceanogr. Res. Pap.* **44**: 955–981.
- JAHNKE, R. A. 1996. The global ocean flux of particulate organic carbon: Areal distribution and magnitude. *Glob. Biogeochem. Cycles* **10**: 71–88.
- , AND M. B. CHRISTIANSEN. 1989. A free-vehicle benthic chamber instrument for sea-floor studies. *Deep-Sea Res. Part I Oceanogr. Res. Pap.* **36**: 625–637.
- , S. R. EMERSON, C. E. REIMERS, J. SCHUFFERT, K. RUTTENBERG, AND D. ARCHER. 1989. Benthic recycling of biogenic debris in the eastern tropical Atlantic Ocean. *Geochim. Cosmochim. Acta* **53**: 2947–2960.
- , AND D. B. JAHNKE. 2004. Calcium carbonate dissolution in deep sea sediments: Reconciling microelectrode, pore water and benthic flux chamber results. *Geochim. Cosmochim. Acta* **68**: 47–59.
- KELL, G. S. 1975. Density, thermal expansivity, and compressibility of liquid water from 0° to 150°C: Correlations and tables for atmospheric pressure and saturation reviewed and expressed on 1968 temperature scale. *J. Chem. Eng. Data* **20**: 97–105.
- LAMPITT, R. S., B. J. BETT, K. KIRIAKOULAKIS, E. E. POPOVA, O. RAGUENEAU, A. VANGRIESHEIM, AND G. A. WOLFF. 2001. Material supply to the abyssal seafloor in the Northeast Atlantic. *Prog. Oceanogr.* **50**: 27–63.
- MARTIN, W. R., AND D. C. MCCORKLE. 1993. Dissolved organic carbon concentrations in marine pore waters determined by high-temperature oxidation. *Limnol. Oceanogr.* **38**: 1464–1479.
- , A. P. MCNICHOL, AND D. C. MCCORKLE. 2000. The radiocarbon age of calcite dissolving at the sea floor: Estimates from pore water data. *Geochim. Cosmochim. Acta* **64**: 1391–1404.
- , AND F. L. SAYLES. 1996. CaCO₃ dissolution in sediments of the Ceara Rise, western equatorial Atlantic. *Geochim. Cosmochim. Acta* **60**: 243–263.
- MOERS, M. E. C., M. BAAS, J. W. DE LEEUW, J. J. BOON, AND P. A. SCHENK. 1990. Occurrence and origin of carbohydrates in peat samples from a mangrove environment, as reflected by abundances of neutral monosaccharides. *Geochim. Cosmochim. Acta* **54**: 2463–2472.
- , J. J. BOON, AND J. W. DE LEEUW. 1989. Carbohydrate speciation and PY-MS mapping of peat samples from a subtropical open marsh environment. *Geochim. Cosmochim. Acta* **53**: 2011–2021.
- MURRAY, J. W., S. EMERSON, AND R. JAHNKE. 1980. Carbonate saturation and the effect of pressure on the alkalinity of interstitial waters from the Guatemala Basin. *Geochim. Cosmochim. Acta* **44**: 963–972.
- PAKULSKI, J. D., AND R. BENNER. 1992. An improved method for the hydrolysis and MBTH analysis of dissolved and particulate carbohydrates in seawater. *Mar. Chem.* **40**: 143–160.
- PAPADIMITRIOU, S., H. KENNEDY, I. BENTALEB, AND D. N. THOMAS. 2002. Dissolved organic carbon in sediments from the eastern North Atlantic. *Mar. Chem.* **79**: 37–47.
- PARK, C. B., AND D. S. CLARK. 2002. Rupture of the cell envelope by decompression of the deep-sea methanogen *Methanococcus jannaschii*. *Appl. Environ. Microbiol.* **68**: 1458–1463.
- PFANNKUCHE, O. 1993. Benthic response to the sedimentation of particulate organic matter at the BIOTRANS station, 47-degrees-N, 20-degrees-W. *Deep-Sea Res. Part II Top. Stud. Oceanogr.* **40**: 135–149.
- , AND T. SOLTWEDEL. 1998. Small benthic size classes along the N.W. European Continental Margin: Spatial and temporal variability in activity and biomass. *Prog. Oceanogr.* **42**: 189–207.
- REIMERS, C. E., K. M. FISCHER, R. MEREWETHER, K. L. SMITH, JR., AND R. A. JAHNKE. 1986. Oxygen microprofiles measured in situ in deep ocean sediments. *Nature (Lond.)* **320**: 741–744.
- ROSENBERG, R., B. HELLMAN, AND A. LUNDBERG. 1996. Benthic macrofaunal community structure in the Norwegian Trench, deep Skagerrak. *J. Sea Res.* **35**: 181–188.
- SAKUGAWA, H., AND N. HANDA. 1983. Chemical studies of dissolved carbohydrates in seawater. Part 1: The concentration and separation of dissolved carbohydrates. *J. Oceanogr. Soc. Jpn.* **39**: 279–288.
- SAYLES, F. L. 1981. The composition and diagenesis of interstitial solutions—II. Fluxes and diagenesis at the water-sediment interface in the high latitude North and South Atlantic. *Geochim. Cosmochim. Acta* **45**: 1061–1086.
- SCHULZ, H. D. 2000. Quantification of early diagenesis: Dissolved constituents in marine pore water, p. 85–128. *In* H. D. Schulz and M. Zabel [eds.], *Marine geochemistry*. Springer Verlag.
- SMITH, K. L. 1992. Benthic boundary-layer communities and carbon cycling at abyssal depths in the central North Pacific. *Limnol. Oceanogr.* **37**: 1034–1056.
- SMITH, K. L., JR., AND K. R. HINGA. 1983. Sediment community respiration in the deep sea, p. 331–370. *In* G. T. Rowe [ed.], *The sea*. Wiley.
- STÄHL, H., P. O. J. HALL, A. TENGBERG, A. B. JOSEFSON, N. STREFTARIS, A. ZENETOS, AND A. KARAGEORGIS. 2004a. Respiration and sequestering of organic carbon in shelf sediments of the oligotrophic northern Aegean Sea. *Mar. Ecol. Prog. Ser.* **269**: 33–48.
- , A. TENGBERG, J. BRUNNEGÅRD, AND P. O. J. HALL. 2004b. Recycling and burial of organic carbon in sediments of the Porcupine Abyssal Plain, NE Atlantic. *Deep-Sea Res. Part I Oceanogr. Res. Pap.* **51**: 777–791.
- , AND OTHERS. 2004c. Factors influencing organic carbon recycling and burial in Skagerrak sediments. *J. Mar. Res.* **62**: 867–907.
- Suess, E., P. J. MULLER, H. S. POWELL, AND C. E. REIMERS. 1980. A close look at nitrification in pelagic sediments. *Geochem. J.* **14**: 129–137.
- TENGBERG, A., H. STÄHL, G. GUST, V. MÜLLER, U. ARNING, H. ANDERSSON, AND P. O. J. HALL. 2004. Intercalibration of benthic flux chambers. I. Accuracy of flux measurements and influence of chamber hydrodynamics. *Prog. Oceanogr.* **60**: 1–28.
- THIEL, H., AND A. L. RICE. 1995. Structure and variability of deep-sea benthos—results from EU funded research. *Int. Rev. Gesamte Hydrobiol.* **80**: 149–383.
- , AND OTHERS. 1988/89. Phytodetritus on the deep-sea floor in a central oceanic region of the Northeast Atlantic. *Biol. Oceanogr.* **6**: 203–239.
- TURLEY, C. M., K. LOCHTE, AND D. J. PATTERSON. 1988. A barophilic flagellate isolated from 4500 m in the mid-North Atlantic. *Deep-Sea Res.* **35**: 1079–1092.
- WEISS, R. F. 1970. The solubility of nitrogen, oxygen, and argon in water and seawater. *Deep-Sea Res.* **17**: 721–735.

- WITBAARD, R., G. C. A. DUINEVELD, J. A. VAN DER WEELE, E. M. BERGHUIS, AND J. P. REYSS. 2000. The benthic response to the seasonal deposition of phytopigments at the Porcupine Abyssal Plain in the North East Atlantic. *J. Sea Res.* **43**: 15–31.
- WITTE, U., AND OTHERS. 2003. In situ experimental evidence of the fate of a phytodetritus pulse at the abyssal sea floor. *Nature* **424**: 763–766.
- YAYANOS, A. A. 2001. Deep-sea piezophilic bacteria, p. 615–637. *In* Methods in microbiology. Marine microbiology. Academic Press.
- , AND A. S. DIETZ. 1983. Death of a hadal deep-sea bacterium after decompression *Science* **220**: 497–498.

Received: 8 December 2005

Accepted: 25 July 2006

Amended: 8 September 2006