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# Bioavailability of organic matter in the sediments of the Porcupine Abyssal Plain, northeastern Atlantic

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ABSTRACT: We investigated spatial and temporal changes in quantity, quality and bioavailability of organic matter in abyssal sediments of the northeastern Atlantic. Sediment samples were collected in the Porcupine Abyssal Plain (PAP, 4800 m depth) during 6 oceanographic cruises from September 1996 to October 1998 down to a depth of 15 cm. Sedimentary proteins, carbohydrates and lipids, and their enzymatically hydrolysable fractions showed significant temporal changes, but different biochemical classes displayed different temporal patterns. Total proteins, carbohydrates and lipids displayed high concentrations, whereas the potentially hydrolysable fractions accounted for only about 10% of their total pools. From September 1996 to October 1998, bioavailable organic carbon concentration in the sediments decreased about 10 gC $m^{-2}$ indicating that this benthic system was not steady state. Hydrolysed proteins and carbohydrates were characterised by different vertical patterns. Carbohydrates increased their relative significance with depth in the sediment indicating a shift of organic matter bioavailability with important trophodynamic implications for subsurface consumers. Vertical profiles of 'reactive' and refractory organic carbon in PAP sediments indicate that organic matter bioavailability in deeper sediment layers is higher than expected from previous theoretical models.

KEY WORDS: Deep-sea sediments · Organic matter · Bioavailability



## INTRODUCTION

Quantity and quality of deep-sea sediment organic matter (OM) are largely dependent upon several factors including origin, composition and biochemical transformations that occur on organic particles during their descent to the ocean floor (Billett et al. 1983, Lochte & Turley 1988, Wakeham et al. 1997, Danovaro et al. 1999).

Defining organic matter quality means discriminating between labile and refractory organic compounds (Mayer 1989). Its composition, indeed, is important both in a biogeochemical perspective (as OM degradation rates might affect its burial in the sediments; Hartnett et al. 1998) and from a trophodynamic point of view (as OM availability influences feeding strategies and the distribution of benthic organisms; Jumars & Penry 1989, Graf 1992). The labile portion of OM mainly consists of simple and/or combined compounds (i.e. biopolymers), and includes carbohydrates, lipids, proteins and nucleic acids that are rapidly mineralised whilst the refractory matter, composed by complex substances like humic and fulvic acids, is slowly broken down (Henrichs 1992). Some labile compounds might become recalcitrant to degradation as a result of the complex interactions occurring with the sedimentary matrix and/or refractory organic macromolecules (Keil et al. 1994).

The determination of the labile fraction of sedimentary organic matter is a difficult task, and a universally accepted method does not exist yet (Dell'Anno et al. 2000). Some authors have tentatively estimated the labile fraction of sedimentary organic matter through

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the determination of the main biochemical classes of organic compounds (i.e. carbohydrates, proteins and lipids), which are assumed to be easier to digest and assimilate (Fichez 1991, Danovaro et al. 1993, Fabiano et al. 1995, Tselepides et al. 2000). However, such an approach could not be efficient as total carbohydrate determination does not discriminate between highly refractory structural components and easily degradable compounds (and/or monomers; Buscail et al. 1995). An alternative approach, based on an enzymatic hydrolysis of sediment samples carried out in the laboratory, has been previously proposed for mimicking OM degradation steps in deposit feeding (George 1964, Mayer et al. 1995, Dauwe et al. 1999). OM susceptible of enzymatic hydrolysis has been recently proposed to represent the potentially bioavailable OM for benthic heterotrophic metabolism (Dell'Anno et al. 2000).

In this study, we adopted this concept of bioavailable organic matter and applied the method based on enzymatic digestion experiments on deep-sea sediments in order to: (1) estimate the potentially bioavailable organic fraction of different biochemical components of sedimentary organic matter; (2) investigate temporal changes in the quality and bioavailability of deep-sea OM in relation to OM inputs from the water column; and (3) investigate changes in OM bioavailability with depth in the sediment core to gather information in the 'optimal foraging theory' perspective (Taghon & Jumars 1984).

## MATERIALS AND METHODS

**Study area and sampling.** Sediment sampling was carried out in the Porcupine Abyssal Plain (PAP, northeastern Atlantic at about 4850 m depth; 48° 50.2'N, 16° 29.9'W) in September 1996, March, July and October 1997, and, March and October 1998. This area is characterised by high sedimentation rates (average settling rate at 3100 m depth 110 ± 30 m $d^{-1}$; Newton et al. 1994) and a strong variability in OM fluxes (Rice et al. 1994). Undisturbed sediment samples were collected using a multicorer (Mod. Maxicorer, i.d., 9.0 cm, depth penetration >20 cm). During each cruise, 4 to 10 cores were taken from 4 to 7 different deployments. Upon recovery all cores were vertically divided into 5 layers: 0 to 5, 10 to 20, 30 to 40, 50 to 60 and 100 to 150 mm and deep frozen at –20°C until analysis. All analyses were performed within 4 to 5 wk after sediment collection.

**Determination of the potentially available proteins.** Details on protein and carbohydrate enzymatic hydrolysis of deep-sea sediment samples are reported in Dell'Anno et al. (2000). Frozen sediment samples were homogenised in 0.1 M Tris, 0.1 M EDTA (pH 7.5) containing 1 mM DTT (dithiothreitol; sediment:buffer ratio of 2.5 w/v) and sonicated 3 times for 1 min (with intervals of 30 s) before enzymes addition. Replicate samples of the slurry (n = 3) from each sediment layer (i.e. treated samples) were added to 100 µl of proteinase-K (1 mg $ml^{-1}$) and 100 µl of protease (600 µg $ml^{-1}$); another set of replicates was added to an equal volume of Tris-EDTA solution without enzymes (i.e. control samples). All samples were incubated for 2 h at 37°C under gentle agitation and subsequently filtered onto GF/F filters and rinsed 2 times with 5 ml of cold 0.1 M Tris-HCl (pH 7.5), in order to remove the digested protein fraction and the enzymes from the sediments. Sediment sub-samples muffled at 550°C for 4 h and processed as describe above were utilised as blanks.

Protein analyses from these samples and from intact sediments were carried out according to Hartree (1972), modified by Rice (1982) to compensate for phenol interference. Protein concentrations were calculated from calibration curves of serum albumin (ranging from 2.5 to 50 µg $ml^{-1}$). Differences between protein concentration of control and treated samples were assumed to represent the concentration of proteins actually hydrolysed by proteases (hydrolysed proteins, HPRT). Total protein concentrations from intact sediments (TPRT) and HPRT concentrations were normalised to sediment dry weight.

**Determination of the potentially available carbohydrates.** For enzymatic digestion of sedimentary carbohydrate pools, frozen sediment samples were homogenised with 0.1 M Na-Phosphate, 0.1 M EDTA (pH 6.9; sediment:buffer ratio of 2.5 w/v) and sonicated 3 times for 1 min (with intervals of 30 s). Replicate samples of the slurry (n = 3, treated samples) were added to 100 µl of α-amylase, 50 µl of β-glucosidase, 100 µl of Proteinase K and 100 µl of lipase (stock solution of all enzymes was 1 mg $ml^{-1}$). Another set of replicates treated adding 0.1 M Na-Phosphate instead of enzyme solutions was utilised as control. Samples were incubated for 2 h at room temperature under gentle agitation. As for protein hydrolysis, sediment sub-samples, muffled at 550°C for 4 h and processed as describe above were utilised as blanks. After incubation, all samples were centrifuged at 2000 × *g* for 10 min and an aliquot of the supernatant was utilised to determine carbohydrates released from the sediments. Soluble carbohydrates were determined from the supernatant of the control sample. Carbohydrates from all supernatants and from intact sediments were analysed spectrophotometrically according to Dubois et al. (1956) and Gerchakov & Hatcher (1972). Carbohydrate concentrations were calculated from calibration curves of D-glucose (from 10 to 200 µg $ml^{-1}$). The actual fraction of hydrolysed carbohydrates (HCHO) was obtained by the difference between the carbohydrate concentrations determined in the supernatant of samples con-

taining enzymes and the soluble fraction of the control. Total carbohydrate concentrations from intact sediments (TCHO) and HCHO concentrations were normalised to sediment dry weight.

**Determination of lipids.** The procedure utilised for protein digestion was also carried out to analyse the sedimentary lipid fraction hydrolysable by a lipase treatment (Triacylglycerol lipase, EC 3.1.1.3 Sigma-Aldrich). However, enzymatically hydrolysed lipid concentrations were very low (<10 µg $g^{-1}$ in the 5 mm layer of sediments collected in September 1996) and undetectable below 5 mm depth and in the other sampling periods. Since a certain fraction of lipids is hydrophobic, these results could be influenced by the inefficacy of the rinsing step in removing enzymatically hydrolysed lipids. The difficulties we found in the enzymatic attack are consistent with results by Santos et al. (1994) who reported large amounts of lipids associated to the more recalcitrant fraction of sedimentary OM in PAP sediments. Our results are consistent with those reported by Galeron et al. (in press) who found a very low content of fatty acids (400 to 6000 ng $g^{-1}$) analysed by gas-chromatography/mass spectrometry.

Total lipids were extracted from sediment samples by direct elution with chloroform and methanol (1:2 v/v) following the procedure of Bligh & Dyer (1959) and analysed according to Marsh & Weinstein (1966). All analyses were carried out on 3 to 4 replicates per sediment horizon. The same sediments previously treated at 550°C for 4 h were utilised as blanks. Lipid concentrations were calculated from calibration curves of tripalmitine (from 5 to 100 µg $ml^{-1}$) and normalised to sediment dry weight.

**Biopolymeric and bioavailable organic carbon.** Biopolymeric organic carbon (BPC; sensu Fabiano et al. 1995) was defined as the sum of the carbon equivalents of total carbohydrates, proteins and lipids (utilising conversion factors of 0.4, 0.49 and 0.75, respectively). Bioavailable organic carbon (BAOC) was defined as the sum of the carbon equivalents of hydrolysable carbohydrates and proteins, assuming the negligible contribution of the hydrolysable lipids.

**Data analysis.** A Spearman rank correlation analysis was performed to test for possible relationships among the investigated variables. Analyses of variance (ANOVA) were carried out to test for temporal and spatial differences in the investigated variables.

## RESULTS

### Total proteins, carbohydrates and lipids

Temporal changes in protein, carbohydrate and lipid concentrations in the top 5 mm of the sediment are reported in Fig. 1. Protein, carbohydrate and lipid concentrations were characterised by significant temporal changes ($p < 0.01$ for the 3 variables) and generally displayed different temporal patterns. Total protein concentrations in the top 5 mm of the sediment were highest in September 1996 (1422.3 ± 23.1 µg $g^{-1}$) and lowest in July 1997 (614.3 ± 76.7 µg $g^{-1}$), whereas total carbohydrates doubled from July 1997 to March 1998 (1194.2 ± 171.6 and 2210.1 ± 39.5 µg $g^{-1}$, respectively). Total lipids reached highest values in October 1998 (775.2 ± 24.0 µg $g^{-1}$) and lowest in March 1997 (140.0 ± 19.5 µg $g^{-1}$). We estimated that each multicorer deployment could occur in a range of about 1 mile, so that the low coefficient of variation for all variables (on average ca 10%; here expressed as standard deviation/mean × 100) refers to this spatial variability.

On average for the 6 sampling periods, total carbohydrate, protein and lipid carbon accounted in the top 5 mm of the sediment for 15 ± 2, 12 ± 2 and 6 ± 2%, respectively, of the total organic carbon pool (TOC data summarised from Mackenzie et al. 1999).

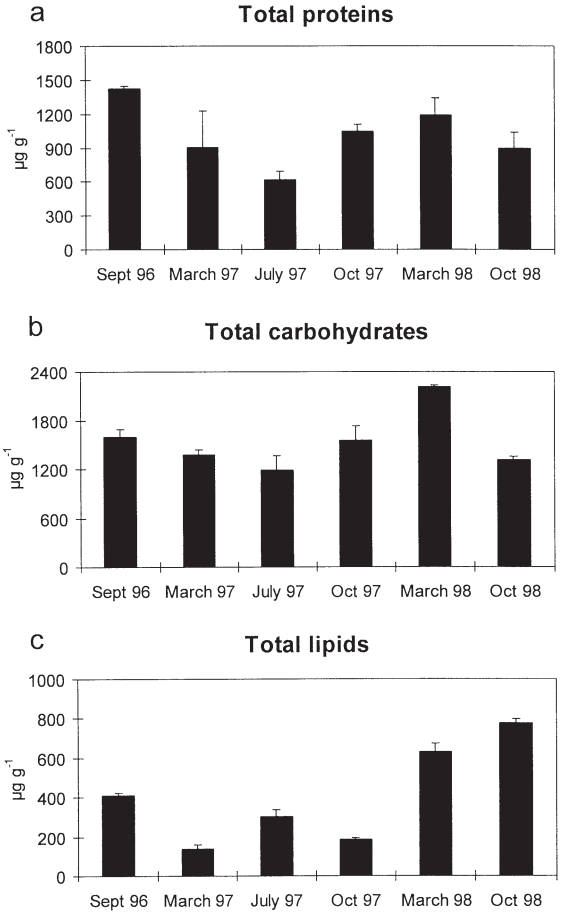


Fig. 1. Temporal changes in total protein (a), carbohydrate (b) and lipid (c) concentrations in the top 0 to 5 mm of sediment. Standard errors are reported

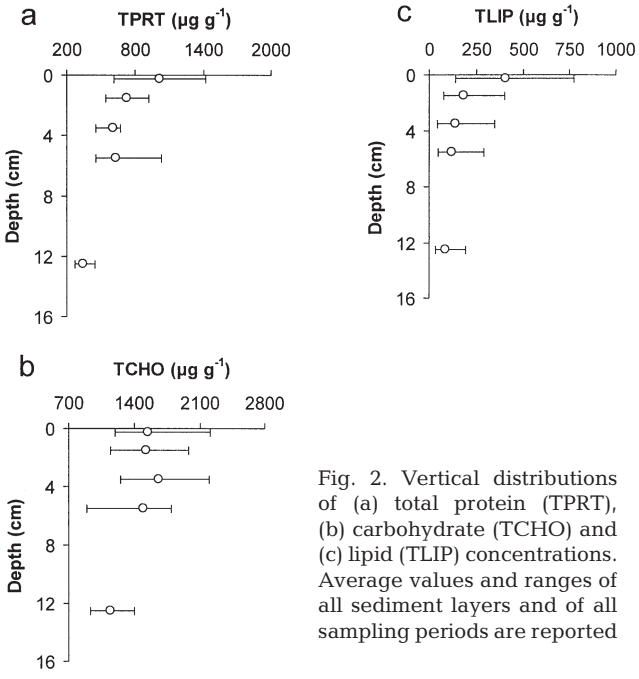


Fig. 2. Vertical distributions of (a) total protein (TPRT), (b) carbohydrate (TCHO) and (c) lipid (TLIP) concentrations. Average values and ranges of all sediment layers and of all sampling periods are reported

Vertical distributions of protein, carbohydrate and lipid concentrations in the sediment core are illustrated in Fig. 2. The 3 variables were characterised by a significant decrease with increasing depth in the sediment ($p < 0.01$ for proteins and lipids, and $p < 0.05$ for carbohydrates). However, protein and lipid concentrations sharply decreased from the top 0 to 5 mm of sediment to the deepest sediment layers (on average for the entire data set, 3- and 5-fold, respectively), whilst carbohydrate concentrations, more conservative, decreased by about 25% from the 0 to 5 to the 100 to 150 mm section of the sediment core.

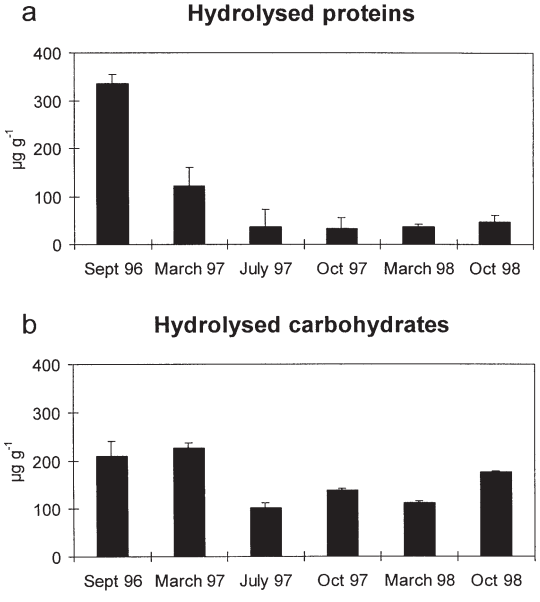


Fig. 3. Temporal changes in hydrolysed protein (a) and carbohydrate (b) concentrations in the top 0 to 5 mm of sediment. Standard errors are reported

### Hydrolysed proteins and carbohydrates

Hydrolysed protein and carbohydrate concentrations were characterised by significant temporal changes ($p < 0.01$; Fig. 3). Highest HPRT concentrations were observed in September 1996 (335.3 ± 20.2 µg $g^{-1}$) which then decreased by about 90% in October 1997; HCHO reached highest values in March 1997 (227.1 ± 10.2 µg $g^{-1}$) and lowest in July 1997 (102.2 ± 10.9 µg $g^{-1}$). In the upper sediment layer (0 to 5 mm), both HPRT and HCHO concentrations accounted on average for 10% of their total pools.

Significant differences in HPRT and HCHO concentrations were observed among sediment layers ($p < 0.05$; Fig. 4). HPRT concentrations decreased 10-fold from the top 5 mm of sediment (on average for all sampling periods, 101.7 ± 44.5 µg $g^{-1}$) to the deepest sediment layers (i.e., 100 to 150 mm, 10.1 ± 3.5 µg $g^{-1}$), whilst HCHO concentrations decreased by only about 30%.

### Biopolymeric and bioavailable organic carbon

Temporal changes in biopolymeric and bioavailable organic carbon concentrations were different (Fig. 5). BPC concentrations in the 0 to 5 mm of sediment were relatively high (on average 1418.4 ± 122.6 µg $g^{-1}$) varying from 1003.9 to 1938.6 µg $g^{-1}$ in July 1997 and March 1998, respectively. BAOC concentrations decreased by about 4-fold from September 1996 to July 1997 and accounted on average for all sampling periods for less than 10% of BPC pools, whereas BPC accounted for 33% of TOC concentrations. BPC and

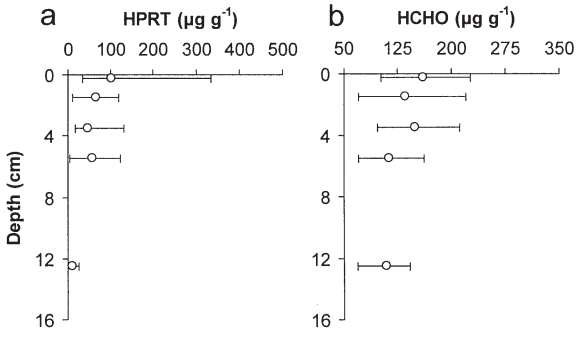


Fig. 4. Vertical distributions of (a) hydrolysed protein (HPRT) and (b) carbohydrate (HCHO) concentrations. Average values and ranges of all sediment layers and of all sampling periods are reported

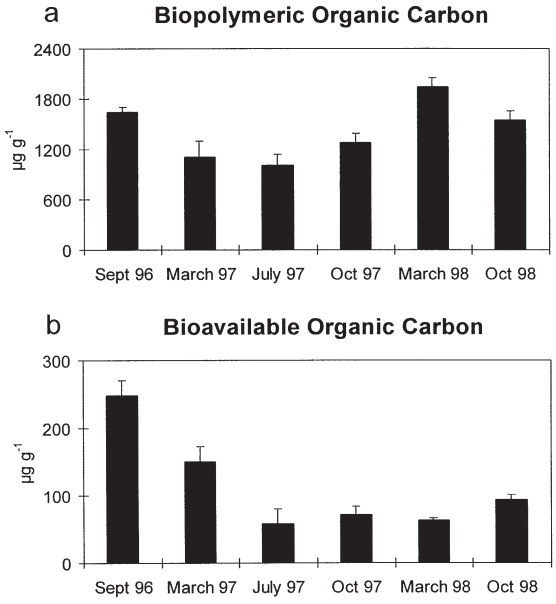


Fig. 5. Temporal changes in (a) biopolymeric and (b) bioavailable organic carbon concentrations in the top 0 to 5 mm of sediment. Standard errors are reported

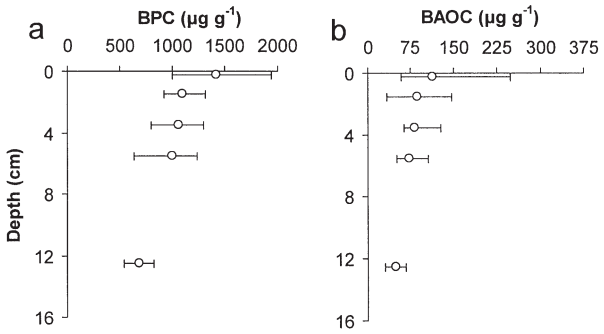


Fig. 6. Vertical distributions of (a) biopolymeric (BPC) and (b) bioavailable organic carbon (BAOC) concentrations. Average values and ranges of all sediment layers and of all sampling periods are reported

BAOC decreased significantly from the top 5 mm to the deepest sediment layers ($p < 0.01$ and $p < 0.05$ for BPC and BAOC, respectively; Fig. 6). Carbohydrates were the dominant component of BPC accounting in the top 5 mm of sediment for 45%, followed by proteins (35%) and lipids (20%). Carbohydrate contribution to BPC pool increased by up to about 70% in the deepest sediment layer, where hydrolysed carbohydrates accounted for >90% of the BAOC pool.

## DISCUSSION

### Bioavailable fraction of OM in PAP sediments

The biochemical composition of the sedimentary organic matter could be assumed as an estimate of the material potentially available to benthic consumers (Fichez 1991, Danovaro et al. 1993, Fabiano et al. 1995, Tselepides et al. 2000). Sedimentary protein, carbohydrate and lipid concentrations reported in this study were high when compared to deep-sea values collected worldwide (Sibuet 1984, Pfannkuche & Thiel 1987, Danovaro et al. 1993, Boetius et al. 1996, Tselepides et al. 2000), indicating that the Porcupine Abyssal Plain is characterised by trophic conditions typical of shelf environments. This is not surprising since the PAP area is characterised by a large phytodetritus deposition to the sea floor (Rice et al. 1986, 1994, Thiel et al. 1988/1989). Organic compounds resistant to biological degradation are easily accumulated in the sediments (Rowe et al. 1990). Proteins and carbohydrates enzymatically hydrolysed (assumed to be generally available to benthic deposit feeders; Mayer et al. 1995, Dell'Anno et al. 2000) in PAP sediments accounted only for a minor fraction (about 10%) of their respective total pools indicating that TPRT and TCHO do not represent the actual available fraction of OM (i.e. digestible by heterotrophs).

Previous studies reported that the present approach for estimating bioavailable OM from frozen sediments might overestimate the bioavailable fraction (Mayer et al. 1995, Dauwe et al. 1999). Dell'Anno et al. (2000) stressed also that since enzyme activities are maximised for temperature and pH, all values should be considered as estimates of the potential OM bioavailability.

In PAP sediments, BAOC concentrations were significantly related with BPC content (Fig. 7; $n = 30$, $r = 0.417$, $p < 0.05$), even though they accounted for less than 10% of BPC pools. For coastal sediments, George (1964) reported that about 14% of the total organic carbon is hydrolysed by enzymes. As in the top 5 mm of the sediment, BPC concentrations accounted for 33% of the total organic carbon content (on average 4.6 ± 0.2 mg $g^{-1}$ for the entire study period); these results indicate that in deep-sea sediments, a minor fraction of total organic carbon pool is actually available to ben-

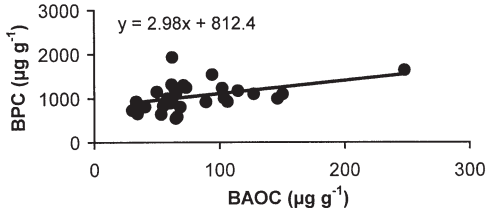


Fig. 7. Relationship between bioavailable (BAOC) and biopolymeric (BPC) organic carbon concentrations in the PAP sediments at each depth and in all sampling periods

thic consumers. This finding strongly supports the conclusion drawn by Fabiano et al. (1995), that total sediment organic carbon does not represent an estimate of the actual food availability to the benthos.

### Temporal changes in the quality and bioavailability of OM

All the investigated variables showed significant temporal changes, whilst total organic carbon concentrations were highly conservative (Mackenzie et al. 1999). These results are in agreement with data reported from long-term temporal series carried out in coastal sediments (Fabiano et al. 1995), and indicate that temporal changes and interannual variability of organic content in deep-sea sediments are evident only when the OM biochemical composition is investigated.

Total protein, carbohydrate and lipid pools displayed different temporal patterns. Synoptic studies reported that seasonal changes in quantity and composition of particle fluxes were very similar for all biochemical classes of organic compounds (Table 1; flux data from Fabiano et al. in press), indicating that in the PAP area, changes observed in sediment organic matter are uncoupled with their respective inputs from the water column. Therefore, it is likely that different rates of accumulation and/or degradation characterise the different classes of organic compounds when particle fluxes reach the sediment surface. This is not surprising since proteins are preferentially utilised by benthic consumers (Tenore 1988, Danovaro et al. 1999) and represent the limiting compound in most deep-sea environments (Deming & Baross 1993). In this regard, hydrolysed proteins are by far the most temporally variable class of organic compounds.

Deep-sea environments are generally assumed to be in a steady state. However, *in situ* measurements of $CO_2$ and dissolved organic carbon proved the presence of a negative balance of C inputs vs outputs from the PAP sediments (Rabouille et al. in press). From September 1996 to October 1998, BAOC concentrations in the top 15 cm of the sediment decreased by about 9 gC $m^{-2}$. In the same period, we observed that protein and carbohydrate carbon fluxes were cumulatively equivalent to about 1 gC $m^{-2}$ (from synoptic data reported by Fabiano et al. in press). Therefore, labile organic compounds could represent the reservoir directly utilised by deep-sea benthic organisms during periods of limited organic matter supply. This was the case in our study in 1997, when no appreciable amounts of phytodetritus were detected by bathysnap observations (Bett et al. in press).

### Vertical distribution of the bioavailable OM: trophic implications

The analysis of the vertical distribution of the different biochemical classes of organic compounds highlighted clear differences between surface and deep sediment layers. In the top 5 mm of the sediment, HPRT accounted for 10% of TPRT whereas their contribution decreased to 3% in the 100 to 150 mm sediment layer. By contrast, HCHO accounted for about 10% of TCHO throughout the sediment core. These data indicate that different organic compounds might play different roles in different sediment layers. In the surface sediments, hydrolysable proteins and carbohydrates represent a roughly equivalent source of bioavailable carbon whereas in deeper sediment layers carbohydrates represent the almost entire food source. These results might have profound implications for benthic trophodynamics. According to the optimal foraging theory, limivorous organisms (i.e., subsurface deposit feeders, which usually feed beneath the sediment mixing depth, ca 4 to 5 cm in the PAP sediments; Patching et al. in press) can compensate the low amount of available OM in deeper sediment layers,

Table 1. Temporal patterns of protein and carbohydrate fluxes at 3000 m depth (integrated to 1 mo before sediment sampling) and the concentration of proteins and carbohydrates in the top 0 to 5 mm of sediment in the Porcupine Abyssal Plain. SE = standard error; na = not available

| Sampling period | Labile organic matter fluxes | | | | Sediment organic matter | | | |
|---|---|---|---|---|---|---|---|---|
| | Carbohydrates | | Proteins | | Carbohydrates | | Proteins | |
| | mgC $m^{-2}$ $d^{-1}$ | SE | mgC $m^{-2}$ $d^{-1}$ | SE | mgC $g^{-1}$ | SE | mgC $g^{-1}$ | SE |
| Sep 1996 | 1.16 | na | 0.15 | na | 0.64 | 0.03 | 0.70 | 0.01 |
| Mar 1997 | 0.27 | 0.08 | 0.04 | 0.03 | 0.55 | 0.02 | 0.44 | 0.16 |
| Jul 1997 | 1.40 | 0.45 | 0.44 | 0.28 | 0.48 | 0.07 | 0.30 | 0.04 |
| Oct 1997 | 0.47 | 0.04 | 0.39 | 0.10 | 0.62 | 0.07 | 0.51 | 0.03 |
| Mar 1998 | 0.33 | 0.07 | 0.60 | 0.29 | 0.88 | 0.01 | 0.58 | 0.07 |
| Oct 1998 | 1.60 | 0.44 | 1.47 | 0.52 | 0.53 | 0.01 | 0.44 | 0.07 |

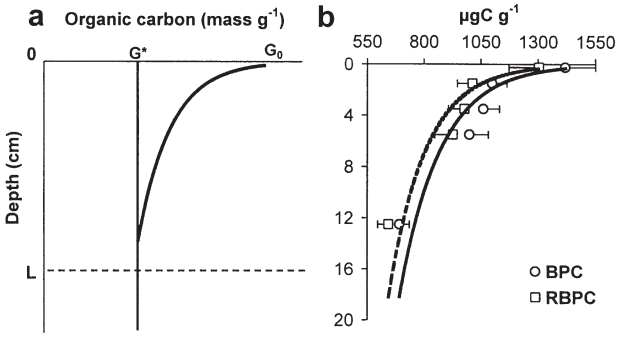


Fig. 8. Comparison between: (a) the Rice & Rhoads (1989) model ($G^*$ is a non-zero asymptotic concentration of organic carbon profiles and $G_0$ is its surface maximum concentration; $L$ is the mixing depth in cm); and (b) the model obtained in this study from the vertical distribution of biopolymeric carbon (BPC) and refractory BPC (i.e., RBPC, as the difference between BPC and BAOC concentrations). Average values (as µgC $g^{-1}$) of all sediment layers and all sampling periods are reported. Standard errors are indicated. Tendency curve equations for BPC (continuous line) and RBPC (broken line) are: BPC = −198.37 ln (depth) + 1288 ($R^2$ = 0.952) and RBPC = −180.12 ln (depth) + 1185.4 ($R^2$ = 0.949)

with a diminished competition for available resources (Jumars et al. 1990). According to our results, subsurface consumers would be also subjected to a different diet regime characterised by a large predominance of carbohydrates and, possibly, different adaptive mechanisms to optimise the exploitation of this trophic source.

The vertical distribution of 'reactive' and refractory (i.e., less rapidly degraded) organic carbon pools (estimated as differences between BPC and BAOC content) in PAP sediments is illustrated in Fig. 8 and compared to the theoretical model proposed by Rice & Rhoads (1989). They proposed that depth profile of OC in the bioturbated zone can be approximated by an exponential function $G(x)$ that decreases with depth x from a surface maximum concentration $G_0$ to a non-zero asymptotic concentration $G^*$. Conversely to that hypothesised by Rice & Rhoads (1989), who assumed a constant ($G_0$; Fig. 8) content of refractory organic carbon with depth in the sediment, our data indicate that the refractory organic carbon pool (and not only the bioavailable fraction) decreases exponentially with depth. Moreover, our results point out that the bioavailable organic carbon in the top 5 mm of the sediments represent a much smaller fraction than the one theoretically calculated from the difference between $G_0$ and $G^*$ (Rice & Rhoads 1989). On the other hand, the bioavailable fraction in the deeper sediment layers, estimated with our approach, is higher than expected, assuming an exponential decrease with depth, as suggested by Rice & Rhoads (1989). These results could be summarised as 'less bioavailable OM in the top and more bioavailable OM in the deep', though of a different quality. These conclusions are obviously the consequence of a different approach focussing on the main biochemical classes of organic compounds instead of on the bulk organic carbon, as in the model proposed by Rice & Rhoads (1989), and further studies are needed to elucidate the mechanisms controlling organic matter bioavailbility in different marine sediments.

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