Biogeosciences Discuss., 9, 17619–17650, 2012
www.biogeosciences-discuss.net/9/17619/2012/
doi:10.5194/bgd-9-17619-2012

Biogeosciences Discussions

Trophic state of sediments from two deep continental margins off Iberia: a biomimetic approach

A. Dell'Anno[1], A. Pusceddu[1], C. Corinaldesi[1], M. Canals[2], S. Heussner[3], L. Thomsen[4], and R. Danovaro[1]

[1]Department of Life and Environmental Science, Polytechnic University of Marche, Via Brecce Bianche, 60131 Ancona, Italy
[2]GRC Geociències Marines, Departament d'Estratigrafia, Paleontologia i Geociències Marines, Facultat de Geologia, Universitat de Barcelona, Campus de Pedralbes, Martí i Franquès s/n, 08028 Barcelona, Spain
[3]CEFREM, UMR5110 CNRS-University of Perpignan, 66860 Perpignan Cedex, France
[4]School of Engineering & Science – SES, Earth and Space Sciences, Jacobs University, Campus Ring 1, 28759 Bremen, Germany

Received: 22 November 2012 – Accepted: 30 November 2012 – Published: 12 December 2012

Correspondence to: A. Dell'Anno (a.dellanno@univpm.it)

Published by Copernicus Publications on behalf of the European Geosciences Union.

Abstract

The trophic state of benthic deep-sea ecosystems can greatly influence key ecological processes (e.g. biomass production and nutrient cycling). Thus, assessing the trophic state of the sediment at different spatial and temporal scales is crucial for a better understanding of deep-sea ecosystem functioning. Here, using a biomimetic approach based on enzymatic digestion of protein and carbohydrate pools, we assess the bioavailability of organic detritus and its nutritional value in the uppermost layer of deep-sea sediments from open slopes and canyons of the Catalan (NW Mediterranean) and Portuguese (NE Atlantic) continental margins, offshore east and west Iberia, respectively. Patterns of sediment trophic state were analyzed in relation to increasing water depth, including repeated samplings over a 3 yr period in the Catalan margin. Bioavailable organic matter and its nutritional value were significantly higher in the Portuguese margin than in the Catalan margin, thus reflecting differences in primary productivity of surface waters reported for the two regions. Similarly, sediments of the Catalan margin were characterized by significantly higher food quantity and quality in spring, when higher primary production processes occur in surface waters, than in summer and autumn. In both continental margins, bioavailable organic C concentrations did not vary or increase with increasing water depth. Differences in the benthic trophic state of canyons against open slopes were more evident in the Portuguese than in the Catalan margin. Overall our findings indicate that deep-sea sediments are characterized by relatively high amounts of bioavailable organic matter. We suggest that the interactions between biological-related processes in surface waters and particle transport and deposition dynamics can play a crucial role in shaping the quantity and distribution of bioavailable organic detritus and its nutritional value along deep continental margins.

1 Introduction

Continental margins play a key role in the C budget and nutrient cycling on a global scale (Liu et al., 2010 and references therein) and represent hot spots of biomass production and biodiversity (Rex et al., 2006; Danovaro et al., 2010; De Leo et al., 2010; McClain and Barry 2010). They can represent either a sink for particulate matter of autochthonous origin (i.e. derived from biological productivity of surface waters and/or exported from the land), or a source of organic material fuelling the deep ocean's interior (Buscail and Germain, 1997; Bauer and Druffel, 1998; Canals et al., 2006; Sampere et al., 2008; Sanchez-Vidal et al., 2008; Masson et al., 2010; Pusceddu et al., 2010). Nevertheless, the extent to which such material is transported/distributed downslope is not consistent along latitudinal or longitudinal gradients, nor constant in time, mainly due to differences in hydrodynamic, topographic, climatic and ecological conditions (Liu et al., 2010). From the topography viewpoint, continental margins are characterized by complex successions of open slopes, submarine canyons and landslide-affected areas (Weaver et al., 2004), whose relative importance on key ecological processes (e.g. biomass production and nutrient cycling) is, however, poorly known, yet. Therefore, identifying factors influencing benthic trophodynamic and biogeochemistry at different spatial and temporal scales is crucial for a better understanding of the functioning of continental margin ecosystems.

There is a general consensus that the trophic state (i.e. food quantity and quality) of deep-sea ecosystems can greatly influence the abundance, biomass and activity of benthic assemblages (from micro- to mega-fauna; Danovaro et al., 1998, 2008a; Gooday, 2002; Smith et al., 2008; Bianchelli et al., 2010), with cascade effects on the provisioning of ecosystem's goods and services (Danovaro et al., 2008b). However, assessing the trophic state of benthic ecosystems is a difficult task since organic detritus is made of a complex array of compounds exhibiting different levels of bioavailability (i.e. from highly labile to refractory compounds, Mayer 1995; Middelburg et al., 1999; Dell'Anno et al., 2000; Dell'Anno and Danovaro 2005; Middelburg and Meysman 2007;

BGD
9, 17619–17650, 2012

Pusceddu et al., 2009). This limits the use of total organic C and N pools as suitable quantitative descriptors of the food availability for consumers (Dell'Anno et al., 2002; Pusceddu et al., 2009), especially in the sediment of continental margins receiving large inputs of land-derived organic material, being potentially more recalcitrant to biodegradation compared to organic compounds of marine origin (Wakeham and Canuel, 2006; Sanchez-Garcia et al., 2009). To overcome this problem, some authors have estimated the labile fraction of organic matter in deep-sea sediments through the determination of the main biochemical classes of organic compounds (i.e. total carbohydrates, proteins and lipids), which are assumed to be easier to digest and assimilate by benthic consumers (Danovaro et al., 1993, 2003; Tselepides et al., 2000; Pusceddu et al., 2010). However, also this approach has some limitations as the analysis of total carbohydrate, for instance, does not discriminate between highly refractory structural components and easily degradable compounds (Buscail et al., 1995; Dell'Anno et al., 2000; Pusceddu et al., 2003). An alternative approach, based on an enzymatic hydrolysis of sediment samples carried out in the laboratory (i.e. biomimetic approach, sensu Mayer et al., 1995), has been proposed for mimicking organic matter degradation steps in deposit feeding (George, 1964; Mayer et al., 1995; Dauwe et al., 1999a). The enzymatically hydrolyzed organic matter pools represent a reliable estimate of the food availability for heterotrophic consumers, thus providing insights on benthic trophodynamics (Dauwe et al., 1999b; Dell'Anno et al., 2000; Pusceddu et al., 2003; Grémare et al., 2005; Mayer et al., 2008; Bourgeois et al., 2011).

Here, using a biomimetic approach, we investigated the bioavailability of organic detritus and its nutritional value in surface deep-sea sediments of open slopes and canyons of the Catalan (NW Mediterranean) and Portuguese (NE Atlantic) continental margins. Topographic differences within the same area (slope vs. canyon) along with differences in ecological and hydrodynamic characteristics of the two continental margins are expected to influence the magnitude and distribution of particle supply to the sea floor, thus providing new insights on factors controlling food availability in the deep sea and related implications on benthic trophodynamics.

BGD
9, 17619–17650, 2012

2 Materials and methods

2.1 Study areas and sampling strategy

Sediment samples have been collected along the Catalan Margin in May 2004, October 2005 and August 2006 at ca. 1000 and 1900 m depth and along the Portuguese margin in September 2006 at depths comprised between ca. 400 and 4200 m (Fig. 1). At all stations triplicate sediment samples were retrieved from three independent deployments of a multi corer. Each sediment core was sliced vertically and the top 1st cm stored in Petri dishes at −20 °C until biochemical analyses. Although the inventory can locally provide estimates of the actual organic matter contents in the sediment that are different from estimates obtained solely from the top surface of the sediment core, the analysis of the top 1st cm has been demonstrated to represent a feasible proxy of the whole trophic state of marine sediments (Pusceddu et al., 2009).

In the Catalan margin, sediments were collected at four stations two of which within the Cap de Creus canyon and the others in the adjacent open slope at similar depths. The Cap de Creus canyon is located in the most western part of the Gulf of Lion, where the shelf narrows and where the wind driven coastal circulation and the Liguro-Provensal or Northern current converge (Millot, 1990). The head of the Cap de Creus canyon is 12 km far from the coastline and extends for 95 km offshore wards and at about 2150 m depth enters the deeper Sete canyon. Recent studies conducted on the Catalan margin reported that the Cap de Creus canyon represents a preferential pathway of particle transport for the entire Gulf of Lion (Palanques et al., 2006) and that dense-shelf water cascading events occurring during winter periods represent one of the main mechanisms of sediment export towards deeper water (Canals et al., 2006; Sanchez-Vidal et al., 2008; Palanques et al., 2012). Primary production in the Gulf of Lion ranges between 78 and 142 $g\,C\,m^{-2}\,yr^{-1}$ (Lefevre et al., 1997).

In the Portuguese margin, sediments were collected at eight stations, four of which located within the Nazaré canyon and the others in the adjacent open slope area. The continental shelf of the Portuguese margin is relatively narrow, with the offshore

BGD
9, 17619–17650, 2012

limit (corresponding to the isobath of 200 m) located 15–30 km from the coastline. The Nazarè canyon, located in the middle part of this margin, is the largest canyon in the area, and intersects the entire continental shelf. The upper and middle canyon collect particles resuspended and transported from the upper shelf and adjacent slope (de Stigter et al., 2007). Intermittent sediment gravity flows have been registered in the canyon, which, coupled to the internal tide circulation produce a net downward canyon transport of particulate material (de Stigter et al., 2007). Primary production values of surface waters in the Portuguese margin vary between 154 and 556 $g\,C\,m^{-2}\,yr^{-1}$ (Alvarez-Salgado et al., 2003). These higher values of primary production when compared with the Gulf of Lion are the result of the prevailing summer upwelling regime characterizing the Portuguese margin (Vitorino et al., 2002).

2.2 Phytopigments and sediment organic matter composition

Chloroplastic pigments (chlorophyll *a* and phaeopigments) were analyzed fluorometrically according to Lorenzen and Jeffrey (1980). Pigments were extracted with 90 % acetone (12 h in the dark at 4 °C). After centrifugation, the supernatant was used to determine the functional chlorophyll *a* and acidified with 0.1 N HCl in order to estimate phaeopigments. Total phytopigment concentrations (CPE) were defined as the sum of chlorophyll *a* and phaeopigment concentrations (Pusceddu et al., 2009).

Total protein (TPRT), carbohydrate (TCHO) and lipid (TLIP) concentrations in the sediment were determined spectrophotometrically as described in details by Danovaro (2010) and concentrations expressed as bovine serum albumin, glucose and tripalmitine equivalents, respectively. For each biochemical assay, blanks were obtained using pre-combusted sediments (450 °C for 4 h). For all of the stations, all analyses were performed on triplicate sediment sub-samples (about 0.5–1 g). Carbohydrate, protein and lipid sediment contents were converted into carbon equivalents using the conversion factors of 0.40, 0.49 and 0.75 $mg\,C\,mg^{-1}$, respectively, and their sum defined as the biopolymeric organic carbon (sensu Fabiano et al., 1995).

BGD
9, 17619–17650, 2012

2.3 Bioavailability and nutritional value of organic matter in the sediments

A biomimetic approach, based on enzymatic hydrolysis of organic matter, was used to determine the bioavailable fraction of the total protein and carbohydrate pools in the sediment. Proteins and carbohydrates were select because they represent the dominant biochemical classes of organic compounds in benthic marine systems worldwide and thus are expected to be the main potential food sources for heterothophic metabolism (Pusceddu et al., 2009). Enzymatically hydrolysable protein and carbohydrate pools in the sediment were determined according to Dell'Anno et al. (2000) with slight modifications. For enzymatic digestion of sedimentary protein pools, frozen sediment samples were homogenized in TRIS-HCl 0.1 M, EDTA 0.1 M buffer (pH 7.5, buffer : sediment ratio of 2.5 volume/weight) and the resulting slurry sonicated three times for 1 min (with intervals of 30 s every min). Triplicate sub-samples of the slurry (treated samples) were added to 100 µL of proteinase K (1 mg mL^{-1}), and 100 µL of protease (600 µg mL^{-1}) solutions. An equal volume of TRIS-HCl 0.1 M, EDTA 0.1 M buffer solution without enzymes (control samples) was added to another set of triplicate sediment subsamples. All samples were incubated for 2 h at room temperature under gentle agitation. Incubation time was selected after checking the highest amount of proteins released enzymatically through time-course experiments carried out on additional sediment sub-samples. After incubation, samples were centrifuged (10 000 × g for 10 min) and the sediments rinsed twice with 5 mL of MilliQ water to remove the digested proteins and the enzymes. Sediment sub-samples muffled at 450 °C for 4 h and processed as describe above were utilized as blanks. Protein analyses from these samples were then carried out according to the procedure described by Danovaro (2010). Differences between protein concentrations of control and treated samples were assumed to account for the proteins actually hydrolyzed by proteases (i.e. enzymatically digestible). Enzymatically hydrolyzed protein concentrations (HPRT) were normalized to sediment dry weight.

BGD
9, 17619–17650, 2012

For enzymatic digestion of sedimentary carbohydrate pools, frozen sediment samples were homogenized with 0.1 M Na-Phosphate, 0.1 M EDTA (pH 6.9; sediment : buffer ratio of 2.5 weight/volume) and sonicated three times for 1 min (with intervals of 30 s). Replicates 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 utilized as control. Samples were incubated for 2 h at room temperature (after checking the highest amount of carbohydrates released enzymatically through time-course experiments) under gentle agitation. As for protein hydrolysis, sediment sub-samples, pre-combusted at 450 °C for 4 h and processed as describe above were utilized as blanks. After incubation, all samples were centrifuged (at 10 000 × g for 10 min) and an aliquot of the supernatant was utilized 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 analyzed spectrophotometrically according to Danovaro (2010). The actual fraction of hydrolyzed carbohydrates was obtained by difference between the carbohydrate concentrations determined in the supernatant of samples containing enzymes and the soluble fraction of the control. Enzymatically hydrolysable carbohydrate concentrations (HCHO) were normalized to sediment dry weight.

Bioavailable organic carbon (BAOC, sensu Danovaro et al., 2001a) was defined as the sum of the carbon equivalents of enzymatically hydrolysable protein and carbohydrate pools.

The nutritional value of organic matter in the sediment was defined on the basis of: (i) the contribution of enzymatically digestible proteins to the BAOC pools since proteins contain essential elements (i.e. nitrogen) and compounds (i.e. aminoacids) for heterotrophic metabolism (Mayer et. al., 1995; Dell'Anno et al., 2000), and (ii) the relative importance of enzymatically digestible organic matter fractions to their total pools (Danovaro et al., 2001a).

BGD
9, 17619–17650, 2012

2.4 Statistical analyses

To test for differences in the quantity of bioavailable organic matter (in terms of HPRT, HCHO and BAOC concentrations) and its nutritional value (as the contribution of enzymatically digestible proteins to the BAOC pools and the relative importance of enzymatically digestible organic matter fractions to their total pools) between canyon and open slope sediments of the Catalan margin in different years and at different depths, univariate 3-way analyses of variance (ANOVA) were carried out. The design included three factors: time (T, with 3 fixed levels: May 2004, October 2005, August 2006), environment (2 fixed levels, canyon vs. open slope) and depth (2 fixed levels, 1000 vs. 1900 m depth).

To test for differences between canyon and open slope sediments in the Portuguese margin at different depths, univariate 2-way analyses of variance (ANOVA) were carried out. The design included two factors: environment (2 fixed levels, canyon vs. open slope) and depth (4 fixed levels, 400, 960, 3200 and 4200 m).

To test for differences between open slopes and canyons of the Catalan and Portuguese margins at similar depths (ca. 1000 m), a one-way ANOVA was carried out. To take into account the effect of sampling time, the analysis was restricted only to sediment samples collected almost synoptically (August 2006 and September 2006 in the Catalan and Portuguese margins, respectively).

Before the ANOVAs, the homogeneity of variances was checked using the Cochran's test on appropriately transformed data, whenever necessary. For those data sets for which the transformation did not allow to obtain homogeneous variances, a more conservative level of significance was considered. When significant differences were encountered, a post-hoc comparison test (at $\alpha = 0.05$) was also carried out. All ANOVA and post-hoc tests were carried out using the PERMANOVA routine included in the Primer 6+ software package.

BGD
9, 17619–17650, 2012

3 Results

3.1 Bioavailability of organic matter in sediments of the Catalan margin

In surface sediments of the Catalan margin, total phytopigment concentrations, here used as a surrogate of the fresh input of primary organic matter, were characterized by significant temporal changes, with values significantly lower in October 2005 than in August 2006 (up to 18.4 ± 0.6 $\mu g\, g^{-1}$ at 1000 m depth in the Cap de Creus canyon; Fig. 2a, Table S1). Sediments collected in the Cap de Creus canyon at 1000 m depth displayed phytopigment contents significantly higher when compared to those of the adjacent open slope at similar depths. In the different sampling periods, total phytopigment concentrations in surface sediments decreased significantly with increasing water depth. Enzymatically hydrolysable protein (HPRT) and carbohydrate (HCHO) concentrations in surface sediments of the Catalan margin are shown in Fig. 2b, c. HPRT concentrations ranged from 33 ± 1 to 268 ± 33 $\mu g\, g^{-1}$ in open slope sediments, and from 74 ± 28 to 482 ± 158 $\mu g\, g^{-1}$ in Cap de Creus sediments. The three-way ANOVA revealed a significant effect of the interaction time × environment × depth on HPRT pools (Table S1). Thus, the post-hoc test revealed that HPRT concentrations were significantly higher in sediments collected in May 2004 than in all other sampling periods, with the exception of samples collected within the canyon at 1000 m depth. No significant differences in HPRT concentrations were generally observed between sediments of the Cap de Creus canyon and those in the adjacent open slope (Table S1).

HCHO concentrations in open slope sediments ranged from 90±10 to 361±38 $\mu g\, g^{-1}$ and from 148±39 to 297±39 $\mu g\, g^{-1}$ in Cap de Creus sediments. The three-way ANOVA revealed a significant effect of the interaction time × environment × depth (Table S1). In October 2005 HCHO concentrations in open slope sediments were significantly higher at 1900 m depth than at 1000 m depth, and viceversa in May 2004. No significant differences were observed between the two environments investigated, except in May 2004 at 1000 m depth, where HCHO concentrations were significantly higher in open slope than in canyon sediments.

BGD
9, 17619–17650, 2012

The contribution of enzymatically hydrolysable proteins to the total protein pools varied from 3 ± 1 to 37 ± 10 %, whereas enzymatically hydrolysable carbohydrates accounted for 7 ± 0.2 to 42 ± 12 % of the total carbohydrate pools (Fig. 3a, b; data on total protein and carbohydrate concentrations are reported in Table S2 of the Supplement). The contribution of enzymatically hydrolysable proteins to the total protein pools in the sediment collected in October 2005 at 1000 m depth were significantly higher than that in the other sampling periods at similar depth. Such a contribution increased significantly with increasing water depth in the sediments of open slope collected in August 2006. Similar patterns were observed for the enzymatically hydrolysable carbohydrates whose contribution significantly increased with water depth in August 2006 both in the open slope and canyon sediments. The fraction of the two enzymatically hydrolysable pools generally did not change significantly between canyon and open slope sediments.

The concentrations of bioavailable C in surface sediments (range: 94–345 $\mu g\, g^{-1}$) were characterized by significant spatial and temporal changes (Fig. 4a, Table S1). The post-hoc test revealed that bioavailable C content in the sediment collected in May 2004 (at 1000 m depth in the open slope and at 1900 m in the canyon) was significantly higher than in the other sampling periods. Slope sediments collected in October 2005 and August 2006 were also characterized by values of bioavailable C concentrations significantly higher at 1900 m depth than at 1000 m depth. The contribution of bioavailable C to the total biopolymeric C pools (range: 6 ± 1–29 ± 7 %) displayed significant temporal and spatial changes with values significantly lower at 1000 m than at 1900 m depth (Fig. 4b, Table S1; data on biopolymeric C are reported in the Supplement). In May 2004 the enzymatically hydrolysable proteins in the sediments represented the dominant component of the bioavailable C pools (on average 60 %), which, conversely, in August 2006 was mainly composed by C associated with enzymatically hydrolysable carbohydrates (on average 70 %; Fig. 4c). The contribution of enzymatically proteins to bioavailable C pools was similar or even significantly higher in the sediments collected at 1900 m depth than in those collected at 1000 m depth (Table S1).

BGD
9, 17619–17650, 2012

3.2 Bioavailability of organic matter in sediments of the Portuguese margin

Total phytopigment concentrations in surface sediments of the Portuguese margin ranged from 3.7±0.1 to 46.9±2.9 µg g^{-1} and were characterized by values significantly higher in the Nazarè canyon than in the adjacent open slope at all depths (Fig. 5a, Table S3). The post-hoc comparison revealed a significant decrease of total phytopigment concentrations with increasing water depth in the canyon and a significant increase in the adjacent open slope (Table S3). In slope sediments HPRT concentrations did not change significantly with increasing water depth, whereas in the canyon significant changes with water depth were observed (Fig. 5b, Table S3). In particular, in the canyon the lowest HPRT concentrations were determined in the sediment collected at 960 m depth (post-hoc $p < 0.01$). Sediments collected within the canyon were also characterized by HPRT concentrations significantly higher than those determined in the adjacent open slope at similar depths. HCHO concentrations were significantly higher in the sediments of the upper part of the canyon and viceversa in the open slope (Fig. 5c, Table S3). The enzymatically hydrolysable carbohydrate pools did not differ significantly between canyon and open slope sediments, with the exception of samples collected at 960 m depth.

In the sediments of the open slope of the Portuguese margin, the contribution of enzymatically hydrolysable proteins to the total protein pools decreased significantly with increasing water depth (Fig. 6a, data on TPRT concentrations are reported in Table S4 of the Supplement). Conversely, in the canyon such a contribution significantly increased with increasing water depth. At shallower depths the contribution of enzymatically hydrolysable proteins to the total protein pools were significantly higher in open slope than in the canyon sediments and viceversa at greater depths. The contribution of enzymatically hydrolysable carbohydrates to the total carbohydrate pools decreased significantly with increasing water depths both in the canyon and in the adjacent open slope (Fig. 6b, data on TCHO concentrations are reported in Table S4

BGD
9, 17619–17650, 2012

of the Supplement). At all depths such a contribution was significantly higher in open slope than in canyon sediments.

Bioavailable C concentrations in surface deep-sea sediments ranged from 218±50 to 680 ± 272 µg g^{-1} (at shallowest depths both in the open slope and the Nazarè canyon; Fig. 7a). Bioavailable C concentrations did not vary significantly with increasing water depth within the canyon, whereas significant lower values in the adjacent open slope were observed at the shallowest depth (Table S3). Canyon sediments were characterized by bioavailable C concentrations significantly higher than those determined in the open slope sediments at similar depths.

The contribution of bioavailable C to the biopolymeric C pools (data on BPC concentrations are reported in Table S4) ranged from 14 ± 1 to 58 ± 6 % and displayed a significant increase with increasing water depth in the canyon (Fig. 7b, Table S3). Conversely, in the open slope such a contribution significantly decreased with increasing water depth. The bioavailable C fraction was significantly higher in the open slope sediments located at shallower depths than that of the canyon sediments at similar depths and viceversa for the deepest station.

The enzymatically hydrolysable proteins accounted, on average, for 58 and 69 % of the bioavailable C pools in open slope and Nazarè canyon sediments, respectively (Fig. 7c). In the sediments of the Nazarè canyon such a contribution significantly increased with increasing water depths (up to 83 % at the deepest station), which, conversely in the open slope significantly decreased (down to 42 % at 3200 m depth; Table S3).

4 Discussion

Primary production in ocean surface waters fuels the deep-sea ecosystems through particle export from the euphotic zone (Dunne et al., 2007). Mechanisms of particle transfer to the sea floor of continental margins depend not only upon particle sedimentation from the upper ocean, but also upon a wide array of processes including down slope and down canyon transport, rebound of re-suspended particles and episodic events such as sediment laden flows and dense shelf water cascading (DSWC; Canals et al., 2006; Heussner et al., 2006; de Stigter et al., 2007). Altogether these factors drive distribution and accumulation of organic matter in surface sediments of continental margins.

In this study differences in primary productivity between surface waters of the two continental margins (ca. 2 to 4-fold higher in the Portuguese margin) were reflected by total phytopigment concentrations, which were significantly higher in the sediments of the Nazarè canyon than in the Cap the Creus despite samples were collected almost synoptically at similar depth. Conversely, slope sediments of the Portuguese margin were characterized by significantly lower phytopigment concentrations than those of the Catalan margin. Such spatial variability of photosynthetically-produced organic matter deposited on surface sediments suggest that the pelagic-benthic coupling mechanisms may be also controlled by the geomorphological characteristics and hydrological processes characterizing the two environments (i.e. canyon vs. open slope).

Previous studies have inferred the amount of labile organic matter in surface deep-sea sediments through the analysis of chlorophyll *a* concentrations (van Oevelen et al., 2011 and 2012). However, chlorophyll *a* is rapidly converted into degradation products during particle sinking to the ocean floor and rapidly decays in the sediments (Fabiano et al., 2001). Moreover, the pool size of labile organic matter in the sediment estimated from chlorophyll *a* concentrations can vary depending on the conversion factor applied (i.e. 30–100 µg C µg chlorophyll a^{-1}; Pusceddu et al., 2009).

In this study we estimated the bioavailability of organic matter in sediments of the Portuguese and Catalan margins through an enzymatic approach. Such an approach, despite its intrinsic limitations, has been extensively used across a wide range of benthic ecosystems to provide quantitative information on food availability for heterotrophic consumers (Mayer et al., 1995 and 2008; Dauwe et al., 1999a; Dell'Anno et al., 2000; Danovaro et al., 2001a; Pusceddu et al., 2003; Grémare et al., 2005; Bourgeois et al., 2011).

BGD
9, 17619–17650, 2012

We found that the enzymatically hydrolyzed protein and carbohydrate pools in the sediments of the Nazarè canyon were 3–4 fold higher than those of the Cap de Creus canyon at similar depth. Also slope sediments of the Portuguese margin were characterized by significantly higher enzymatically hydrolyzed organic matter concentrations when compared to slope sediments of the Catalan margin. The comparison with available literature information indicates that the continental margin sediments investigated in this study are characterized by enzymatically hydrolyzed protein and carbohydrate concentrations similar to those determined in shallow benthic systems (Pusceddu et al., 2003; Mayer et al., 2008 and citations therein for a comparison with results based on different approaches/protocols), but up to 2–3 fold higher than those determined in abyssal sediments of the NE Atlantic Ocean (Dell'Anno et al., 2000; Danovaro et al., 2001a).

Phytodetritus sinking from the water column represent a major vehicle of bioavailable organic matter to the deep-sea floor (Fabiano et al., 2001; Dell'Anno and Danovaro, 2005). In this study we found a significant relationship between enzymatically hydrolyzed protein concentrations and phytopigment contents in the sediments of the Portuguese margin ($n = 8$, $r = 0.723$, $p < 0.05$), though this was not the case for the Catalan margin. High concentrations of non-algal bioavailable organic N compounds (in terms of enzymatically hydrolysable aminoacids) have been documented in benthic systems influenced by major river outflows (Mayer et al., 2008; Bourgeois et al., 2011), including sediments previously collected in the Gulf of Lion (Grémare et al., 2005; Bourgeois et al., 2011). Previous findings based on stable isotope and/or biochemical analyses provided evidence that the Cap de Creus canyon and the adjacent open slope can receive high amounts of organic material of continental origin, especially during DSWC events, like those occurring during winter 2005 and 2006 (Canals et al., 2006; Sanchez-Vidal et al., 2009; Pasqual et al., 2010; Palanques et al., 2012). Therefore, our results suggest that physical processes related with the general circulation pathways along with episodic events involving massive particle transport can greatly influence the Catalan margin not only providing large amounts of lithogenic

BGD
9, 17619–17650, 2012

material (Canals et al., 2006; Heussner et al., 2006; Palanques et al., 2006), but also fuelling the benthic systems with bioavailable N-rich compounds.

Sediments from the open slopes of the two continental margins investigated here were characterized by a significant increase of bioavailable organic C concentrations with increasing water depth. Such depth-related patterns of bioavailable organic matter are consistent with previous studies carried out in the same areas, based on the use of other proxies of sediment trophic state (i.e. total and/or enzymatically hydrolysable aminoacids; Grèmare et al., 2005; García and Thomsen, 2008). No significant differences in bioavailable C concentrations with increasing water depth were observed either in the sediments of the Nazarè canyon or in those of the Cap de Creus canyon. Although the downward transport of particles in the two areas relies on different mechanisms (Heussner et al., 2006; Canals et al., 2006; Palanques et al., 2006; de Stigter et al., 2007; Arzola et al., 2008), our results suggest that hydrodynamic processes able to redistribute material from shallower down to bathyal/abyssal depths may have profound implications on the quantity and distribution of bioavailable C pools on the seafloor.

In this study differences in the trophic state (as bioavailable C pools) between canyons and the adjacent open slopes were more evident in the Portuguese than in the Catalan margin. Bioavailable C concentrations in surface sediments of the Nazarè canyon were, indeed, significantly higher than those in the adjacent open slope (on average, 524 ± 26 vs. $292 \pm 61\ \mu g\ g^{-1}$), whereas no significant differences between environments were generally observed in the Catalan margin. The sediments of the Nazarè canyon were also characterized by a higher nutritional value of bioavailable organic matter than those of the open slope, as revealed by the higher contribution of enzymatically digestible proteins to the BAOC pools. Such trophic characteristics let us to hypothesize, according to the optimal foraging theory (McArthur and Pianka 1966) and after re-examination from the point of view of benthic deposit feeders, that detritus feeders inhabiting the Nazarè canyon can have important energetic/metabolic advantages related to the better quality and higher quantity of bioavailable food than

BGD
9, 17619–17650, 2012

those inhabiting the open slopes. These findings provide important clues to explain why higher macrofaunal abundances are reported in the Nazarè canyon compared with the adjacent open slopes at similar depths (Cunha et al., 2011). Moreover, the enhanced nutritional value of bioavailable organic detritus with increasing water depth within the Nazarè canyon can contribute to explain the distribution patterns of macrofaunal abundances (474 vs. 4599 ind. m^{-2} at 940 and 3200 m depth) and assemblage composition, as previously reported by Cunha et al. (2011).

Despite the limited spatial differences observed comparing canyon vs. open slope in the Catalan margin, significant temporal changes were observed. Bioavailable organic C pools as well as its nutritional value (in terms of the relative importance of enzymatically digested proteins to the bioavailable C pools) were significantly higher in May 2004 than in the other sampling periods in both environments (i.e., the Cap de Creus canyon vs. the adjacent open slope). This difference, also observed in other canyons of the Gulf of Lion (Lopez-Fernandez et al., 2012) may be attributed to the phytoplankton spring bloom reported for the NW Mediterranean (Estrada et al., 1996; Lefevre et al., 1997). We can therefore infer that, according to the optimal foraging theory (McArthur and Pianka 1966), in spring deep-sea detritus feeders would need to ingest less material than in summer/early autumn to get the optimal quantity and quality of labile food. Temporal differences in the nutritional value of bioavailable organic matter pools were also evident when comparing sediments collected at the same depths in October 2005 and August 2006. In particular, bioavailable organic C pools in the sediments collected in October 2005 were mainly represented by labile proteins (on average 55 %) whose contribution significantly decreased in the sediments collected in August 2006 (on average 30 %).

There is an increasing consensus that deep-sea ecosystems are more dynamic than previously hypothesized (Smith and Kaufmann, 1999; Danovaro et al., 2001b; Ruhl and Smith, 2004; Ruhl et al., 2008; Billett et al., 2010) and that important changes in quantity and composition of bioavailable organic matter deposited on the ocean floor occur both at seasonal and inter-annual time scales (Danovaro et al., 2001a; Fabiano

BGD
9, 17619–17650, 2012

et al., 2001; Dell'Anno et al., 2005; Smith et al., 2010). Our results from the Catalan margin reinforce this view and suggest that dense-shelf water cascading events may amplify the temporal variability of the trophic state of benthic deep-sea ecosystems related to changes in biological production of the photic zone. Since DSWC events occur along continental margins around the world oceans (Ivanov et al., 2004; Canals et al., 2009), long-term and wide spatial-scale investigations of bio-geosphere interactions are needed to better understand the impact of these events on the bioavailability of organic matter and related implications on benthic trophodynamics and ecosystem functioning.

Supplementary material related to this article is available online at: http://www.biogeosciences-discuss.net/9/17619/2012/ bgd-9-17619-2012-supplement.pdf.

Acknowledgement. This study has been conducted in the framework of the European funded Projects HERMES (Hot Spot Ecosystem Research on the Margins of European Seas; GOCE-CT-2005-511234-1) and HERMIONE (Hotspot Ecosystem Research and Man's Impact On European Seas; contract n. 226354) and the Spanish project DOS MARES (CTM2010-21810-C03-01). University of Barcelona researchers benefited from grant 2009SGR1305 by Generalitat de Catalunya to excellence research groups. The authors are indebted with the crews of the ships Pelagia (The Netherlands), Urania (Italy) and Thetis II (France) for their valuable help during field activities.

References

Alvarez-Salgado, X. A., Figueiras, F. G., Perez, F. F., Groom, S., Nogueira, E., Borges, A. V., Chou, L., Moncoiffé, G., Rıos, A. F., Miller, A. E. J., Frankignoulle, M., Savidge, G., and Wollast, R.: The Portugal coastal counter current off NW Spain: new insights on its biogeochemical variability, Prog. Oceanogr., 56, 281–321, 2003.

BGD
9, 17619–17650, 2012

Arzola, R. G., Wynn, R. B., Lastras, G. B., Masson, D. G., and Weaver, P. P. E.: Sedimentary features and processes in the Nazaré and Setubal submarine canyons, west Iberian margin, Mar. Geol., 250, 64–88, 2008.
Bauer, J. E. and Druffel, E. R. M.: Ocean margins as a significant source of organic matter to the deep open ocean, Nature, 392, 482–485, 1998.
Bianchelli, S., Gambi, C., Zeppilli, D., and Danovaro, R.: Metazoan meiofauna in deep-sea canyons and adjacent open slopes: a large-scale comparison with focus on the rare taxa, Deep-Sea Res. I, 57, 420–433, 2010.
Billett, D. S. M., Bett, B. J., Reid, W. D. K., Boorman, B., and Priede, M.: Long-term change in the abyssal NE Atlantic: The "Amperima Event" revisited, Deep-Sea Res. Pt. II, 57, 1406–1417, 2010.
Bourgeois, S., Pruski, A. M., Sun, M.-Y., Buscail, R., Lantoine, F., Kerhervé, P., Vétion, G., Riviére, B., and Charles, F.: Distribution and lability of land-derived organic matter in the surface sediments of the Rhône prodelta and the adjacent shelf (Mediterranean Sea, France): a multi proxy study, Biogeosciences, 8, 3107–3125, doi:10.5194/bg-8-3107-2011, 2011.
Buscail, R. and Germain, C.: Present-day organic matter sedimentation on the NW Mediterranean margin: importance of off-shelf export, Limnol. Oceanogr., 42, 217–229, 1997.
Buscail, R., Pocklington, R., and Germain, C.: Seasonal variability of the organic matter in a sedimentary coastal environment: sources, degradation and accumulation (continental shelf of the Gulf of Lions–northwestern Mediterranean Sea), Cont. Shelf. Res., 15, 843–869, 1995.
Canals, M., Puig, P., Durrieu de Madron, X., Heussner, S., Palanques, A., and Fabres, J.: Flushing submarine canyons, Nature, 444, 354–357, 2006.
Canals, M., Danovaro, R.,. Heussner, S., Lykousis, V., Puig, P., Trincardi, F., Calafat, A. M., Durrieu de Madron, X., Palanques, A., and Sànchez-Vidal, A.: Cascades in Mediterranean submarine grand canyons, Oceanography, 22, 26–43, 2009.
Cunha, M. R., Paterson, G. L. J., Amaro, T., Blackbird, S., de Stigter, H. C., Ferreira, C., Glover, A., Hilário, A., Kiriakoulakis, K., Neal, L., Ravara, A., Rodrigues, C. F., Tiago, Á., and Billett, D. S. M.: Biodiversity of macrofaunal assemblages from three Portuguese submarine canyons (NE Atlantic), Deep-Sea Res. Pt. II, 58, 2433–2447, 2011.
Danovaro, R.: Methods for the Study of Deep-Sea Sediments, Their Functioning and Biodiversity, CRC Press, Taylor & Francis Group, USA, 2010.

Danovaro, R., Fabiano, M., and Della Croce, N.: Labile organic matter and microbial biomasses in deep-sea sediments (Eastern Mediterranean Sea), Deep-Sea Res. Pt. I, 40, 953–965, 1993.
Danovaro, R., Marrale, D., Della Croce, N., Dell'Anno, A., and Fabiano, M.: Heterotrophic nanoflagellates, bacteria and labile organic compounds in continental shelf and deep-sea sediments of the Eastern Mediterranean, Microb. Ecol., 35, 244–255, 1998.
Danovaro, R., Dell'Anno, A., and Fabiano, M.: Bioavailability of organic matter in the sediments of the Porcupine Abyssal Plain, Northeastern Atlantic, Mar. Ecol. Prog. Ser., 220, 25–32, 2001a.
Danovaro, R., Dell'Anno, A., Fabiano, M., Pusceddu, A., and Tselepides, A.: Deep-sea ecosystem response to climate changes: the eastern Mediterranean case study, Trends Ecol. Evol., 16, 505–510, 2001b.
Danovaro, R., Della Croce, N., Dell'Anno, A., and Pusceddu, A.: A depocenter of organic matter at 7800 m depth in the SE Pacific Ocean, Deep-Sea Res. Pt. I, 50, 1411–1420, 2003.
Danovaro, R., Dell'Anno, A., Corinaldesi, C., Magagnini, M., Noble, R., Tamburini, C., and Weinbauer, M.: Major viral impact on the functioning of benthic deep-sea ecosystems, Nature, 454, 1084–1087, 2008a.
Danovaro, R., Gambi, C., Dell'Anno, A., Corinaldesi, C., Fraschetti, S., Vanreusel, A., Vincx, M., and Gooday, A. J.: Exponential decline of deep-sea ecosystem functioning linked to benthic biodiversity loss, Curr. Biol., 18, 1–8, 2008b.
Danovaro, R., Canals, M., Gambi, C., Heussner, S., Lampadariou, N., and Vanreusel, A.: Exploring benthic biodiversity patterns and hotspots on European margin slopes, Oceanography, 22, 16–25, 2010.
Dauwe, B., Middelburg, J. J., Van-Rijswijk, P., Sinke, J., Herman, P. M. J., and Heip, C. H. R.: Enzymatically hydrolyzable amino acids in North Sea sediments and their possible implication for sediment nutritional values, J. Mar. Res., 57, 109–134, 1999a.
Dauwe, B., Middelburg, J. J., Herman, P. M. J., and Heip, C. H. R.: Linking diagenetic alteration of amino acids and bulk organic matter reactivity, Limnol. Oceanogr., 44, 1809–1814, 1999b.
de Stigter, H. C., Boer, W., de Jesus Mendes, P. A., Jesus, C. C., Thomsen, L., van den Bergh, G. D., and van Weering, T. C. E.: Recent sediment transport and deposition in the Nazaré Canyon, Portuguese continental margin, Mar. Geol., 246, 144–164, 2007.

BGD
9, 17619–17650, 2012

Trophic state of sediments from two deep continental margins

A. Dell'Anno et al.

Title Page
Abstract Introduction
Conclusions References
Tables Figures
◀| |▶
◀ ▶
Back Close
Full Screen / Esc
Printer-friendly Version
Interactive Discussion

De Leo, F. C., Smith, C. R., Rowden, A. A., Bowden, D. A., and Clark, M. R.: Submarine canyons: hot spots of benthic biomass and productivity in the deep sea, P. Roy. Soc. B-Biol Sci., 277, 2783–2792, 2010.

Dell'Anno, A. and Danovaro, R.: Extracellular DNA plays a key role in deep-sea ecosystem functioning, Science, 309, 2179, 2005.

Dell'Anno, A., Fabiano, M., Mei, M. L., and Danovaro, R.: Enzymatically hydrolised protein and carbohydrate pools in deep-sea sediments: estimates of the potential bioavailable fraction and methodological considerations, Mar. Ecol. Prog. Ser., 196, 15–23, 2000.

Dell'Anno, A., Mei, M. L., Pusceddu, A., and Danovaro, R.: Assessing the trophic state and eutrophication of coastal marine systems: a new approach based on the biochemical composition of sediment organic matter, Mar. Poll. Bull., 44, 611–622, 2002.

Dell'Anno, A., Corinaldesi, C., Stavrakakis, S., Lykousis, V., and Danovaro, R.: Pelagic-benthic coupling and diagenesis of nucleic acids in a deep-sea continental margin and an open-slope system of the Eastern Mediterranean, Appl. Environ. Microbiol., 71, 6070–6076, 2005.

Dunne, J. P., Sarmiento, J. L., and Gnanadesikan, A.: A synthesis of global particle export from the surface ocean and cycling through the ocean interior and on the seafloor, Global Biogeochem. Cy., 21, GB4006, doi:10.1029/2006GB002907, 2007.

Estrada, M.: Primary production in the northwestern Mediterranean, Sci. Mar., 60, 55–64, 1996.

Fabiano, M., Danovaro, R., and Fraschetti, S.: A three-year time series of elemental and biochemical composition of organic matter in subtidal sandy sediments of the Ligurian Sea (north western Mediterranean), Cont. Shelf Res., 15, 1453–1469, 1995.

Fabiano, M., Pusceddu, A., Dell'Anno, A., Armeni, M., Vanucci, S., Lampitt, R., Wolff, G., and Danovaro, R.: Fluxes of phytopigments and labile organic matter to the deep ocean in the NE Atlantic Ocean, Prog. Oceanogr., 50, 89–104, 2001.

García, R. and Thomsen, L.: Bioavailable organic matter in surface sediments of the Nazaré canyon and adjacent slope (Western Iberian Margin), J. Mar. Syst., 74, 44–59, 2008.

George, J. D.: Organic matter available to the polychaete *Cirriformia tentaculata* (Montagu) living in an intertidal mud flat, Limnol. Oceanogr., 9, 453–455, 1964.

Gooday, A. J.: Biological responses to seasonally varying fluxes of organic matter to the ocean floor: a review, J. Oceanogr., 58, 305–332, 2002.

BGD
9, 17619–17650, 2012

Trophic state of sediments from two deep continental margins

A. Dell'Anno et al.

Title Page
Abstract | Introduction
Conclusions | References
Tables | Figures
◀| |▶
◀ ▶
Back | Close
Full Screen / Esc
Printer-friendly Version
Interactive Discussion

Grémare, A., Gutiérrez, D., Anschutz, P., Amouroux, J. M., Deflandre, B., and Vétion, G.: Spatio-temporal changes in totally and enzymatically hydrolyzable amino acids of superficial sediments from three contrasted areas, Prog. Oceanogr., 65, 89–111, 2005.

Heussner, S., Durrieu de Madron X., Calafat A., Canals, M., Carbonne, J., Delsaut, N., and Saragoni, G.: Spatial and temporal variability of downward particle fluxes on a continental slope: Lessons from an 8-yr experiment in the Gulf of Lions (NW Mediterranean), Mar. Geol., 234, 63–92, 2006.

Ivanov, V. V., Shapiro, G. I., Huthnance, J. M., Aleynik, D. L., and Golovin, P. N.: Cascades of dense water around the world ocean, Progr. Oceanogr., 60, 47–98, 2004.

Lefevre, D., Minas, H. J., Minas, M., Robinson, C., Williams, P. J. L. E. B., and Woodward, E. M. S.: Review of gross community production, primary production, net community production and dark community respiration in the Gulf of Lions, Deep-Sea Res., 44, 801–832, 1997.

Liu, K.-K., Atkinson, L., Quiñones, R., and Talaue-McManus, L.: Carbon and Nutrient Fluxes in Continental Margins: a Global Synthesis, Springer-Verlag, Berlin, Heidelberg, 2010.

López-Fernández, P., Bianchelli, S., Pusceddu, A., Calafat, A., Danovaro, R., Canals, M.: Bioavailable compounds in sinking particulate organic matter, Blanes Canyon, NW Mediterranean Sea: effects of a large storm and sea surface biological processes, Progr. Oceanogr., in press, 2012.

Lorenzen, C. and Jeffrey, J.: Determination of chlorophyll in seawater, Technical Paper in Marine Science (UNESCO), 35, 1–20, 1980.

Masson, D. G., Huvenne, V. A. I., de Stigter, H. C., Wolff, G. A., Kiriakoulakis, K., Arzola, R. G., and Blackbird, S.: Efficient burial of carbon in a submarine canyon, Geology, 38, 831–834, 2010.

Mayer, L. M.: Sedimentary organic matter preservation: an assessment and speculative synthesis - a comment, Mar. Chem., 49, 123–126, 1995.

Mayer, L. M., Schick, L. L., Sawyer, T., Plante, C. J., Jumars, P. A., and Self, R. L.: Bioavailable amino acids in sediments: a biomimetic, kinetics-based approach, Limnol. Oceanogr. 40, 511–520, 1995.

Mayer, L. M., Schick, L. L., and Allison, M. A.: Input of nutritionally rich organic matter from the Mississippi river to the Louisiana coastal Zone, Estuar. Coast., 31, 1052–1062, 2008.

MacArthur, R. H. and Pianka, E. R.: On the optimal use of a patchy environment, Am. Nat., 100, 603–609, 1966.

BGD

9, 17619–17650, 2012

McClain, C. R. and Barry, J. P.: Habitat heterogeneity, disturbance, and productivity work in concert to regulate biodiversity in deep submarine canyons, Ecology, 91, 964–976, 2010.
Middelburg, J. J. and Meysman, F. J. R.: Burial at sea, Science, 317, 1294–1295, 2007.
Middelburg, J. J., Nieuwenhuize, J., and van Breugel, P.: Black carbon in marine sediments, Mar. Chem., 65, 245–252, 1999.
Millot, C.: The Gulf of Lions' hydrodynamics, Cont. Shelf Res., 10, 885–894, 1990.
Palanques, A., Durrieu de Madron, X., Puig, P., Fabres, J., Guillén, J., Calafat, A., Canals, M., Heussner, S., and Bonnin, J.: Suspended sediment fluxes and transport processes in the Gulf of Lions submarine canyons. The role of storms and dense water cascading, Mar. Geol., 236, 43–61, 2006.
Palanques, A., Puig, P., Durrieu de Madron, X., Sanchez-Vidal, A., Pasqual, C., Martín, J., Calafat, A., Heussner, S., and Canals, M.: Sediment transport to the deep canyons and open-slope of the western Gulf of Lions during the 2006 intense cascading and open-sea convection period, Progr. Oceanogr., 106, 1–15, 2012.
Pasqual, C., Sanchez-Vidal, A., Zúñiga, D., Calafat, A., Canals, M., Durrieu de Madron, X., Puig, P., Heussner, S., Palanques, A., and Delsaut, N.: Flux and composition of settling particles across the continental margin of the Gulf of Lion: the role of dense shelf water cascading, Biogeosciences, 7, 217–231, doi:10.5194/bg-7-217-2010, 2010.
Pusceddu, A., Dell'Anno, A., Danovaro, R., Manini, E., Sarà, G., and Fabiano, M.: Enzymatically hydrolyzable protein and carbohydrate sedimentary pools as indicators of the trophic state of "detritus sink" systems: a case study in a Mediterranean coastal lagoon, Estuaries, 26, 641–650, 2003.
Pusceddu, A., Dell'Anno, A., Fabiano, M., and Danovaro, R.: Quantity, biochemical composition and bioavailability of sediment organic matter as complementary signatures of benthic trophic status, Mar. Ecol. Prog. Ser., 375, 41–52, 2009.
Pusceddu, A., Bianchelli, S., Sanchez Vidal, A., Canals, M., Durrieu De Madron, X., Heussner, S., Lykousis, V., de Stigter, H., Trincardi, F., and Danovaro, R.: Organic matter in sediments of canyons and open slopes in the Eastern Atlantic and Mediterranean continental margins, Deep-Sea Res. Pt. I, 57, 441–457, 2010.
Rex, M. A., Etter, R. J., Morris, J. S., Crouse, J., McClain, C. R., Johnson, N. A., Stuart, C. T., Thies, R., and Avery, R.: Global bathymetric patterns of standing stock and body size in the deep-sea benthos, Mar. Ecol. Progr. Ser., 317, 1–8, 2006.

BGD
9, 17619–17650, 2012

Trophic state of sediments from two deep continental margins

A. Dell'Anno et al.

Ruhl, H. A. and Smith, K. L.: Shifts in deep-sea community structure linked to climate and food supply, Science, 305, 513–515, 2004.
Ruhl, H. A., Ellena, J. A., and Smith Jr., K. L.: Connections between climate, food limitation, and carbon cycling in abyssal sediment communities: a long time-series perspective, P. Natl. Acad. Sci. USA, 105, 17006–17011, 2008.
Sampere, T. P., Bianchi, T. S., Wakeham, S. G., and Allison, M. A.: Sources of organic matter in surface sediments of the Louisiana Continental margin: effects of major depositional/transport pathways and hurricane Ivan, Cont. Shelf Res., 28, 2472–2487, 2008.
Sanchez-Garcia, L., de Andres, J. R., Martin-Rubi, J. A., and Louchouarn, P.: Diagenetic state and source characterization of marine sediments from the inner continental shelf of the Gulf of Cadiz (SW Spain), constrained by terrigenous biomarkers, Org. Geochem., 40, 184–194, 2009.
Sanchez-Vidal, A., Pasqual, C., Kerhervé, P., Calafat, A., Heussner, S., Palanques, A., Durrieu de Madron, X., Canals, M., and Puig, P.: Impact of dense shelf water cascading on the transfer of organic matter to the deep western Mediterranean basin, Geophys. Res. Lett., 35, 1–5, 2008.
Sanchez-Vidal, A., Pasqual, C., Kerhervé, P., Heussner, S., Calafat, A., Palanques, A., Durrieu de Madron, X., Canals, M., and Puig, P.: Across margin export of organic matter by cascading events traced by stable isotopes, northwestern Mediterranean Sea, Limnol. Oceanogr., 54, 1488–1500, 2009.
Smith, C. R., De Leo, F. C., Bernardino, A. F., Sweetman, A. K., and Martinez Arbizu, P.: Abyssal food limitation, ecosystem structure and climate change, Trends Ecol. Evol., 23, 518–528, 2008.
Smith, K. L. and Kaufmann, R. S.: Long-term discrepancy between food supply and demand in the deep-eastern North Pacific, Science, 284, 1174–1177, 1999.
Smith, K. L., Ruhl, H. A., Bett, B. J., Billett, D. S. M., Lampitt, R. S., and Kaufmann, R. S.: Climate, carbon cycling, and deep-ocean ecosystems, P. Natl. Acad. Sci., 106, 19211–19218, 2010.
Tselepides, A., Polychronaki, T., Marrale, D., Akoumianaki, I., Dell'Anno, A., Pusceddu, A., and Danovaro, R.: Organic matter composition of the continental shelf and bathyal sediments of the Cretan Sea (NE Mediterranean), Prog. Oceanogr., 46, 311–344, 2000.

BGD
9, 17619–17650, 2012

van Oevelen, D., Soetaert, K., García Novoa, R., de Stigter, H., da Cunha, M., Pusceddu, A., and Danovaro, R.: Canyon conditions impact carbon flows in food webs of three sections of the Nazaré canyon, Deep-Sea Res. Pt. II, 58, 2461–2476, 2011.
van Oevelen, D., Soetaert, K., Heip, C.: Carbon flows in the benthic food web of the Porcupine Abyssal Plain: the (un)importance of labile detritus in supporting microbial and faunal carbon demands, Limnol. Oceanogr., 57, 645–664, 2012.
Vitorino, J., Oliveira, A., Jouanneau, J. M., and Drago, T.: Winter dynamics on the northern Portuguese shelf. Part 1: Physical processes, Prog. Oceanogr., 52, 29–153, 2002.
Wakeham, S. G. and Canuel, E. A.: Degradation and preservation of organic matter in marine sediments, in: The Handbook of Environmental Chemistry, edited by: Volkman, J. K., 295–321, Springer, Berlin, Heidelberg, 2006.
Weaver, P. E., Billett, D. M., Boetius, A., Danovaro, R., Freiwald, A., and Sibuet, M.: Hotspot ecosystem research on Europe's deep-ocean margins, Oceanography, 17, 132–143, 2004.

BGD
9, 17619–17650, 2012

Trophic state of sediments from two deep continental margins

A. Dell'Anno et al.

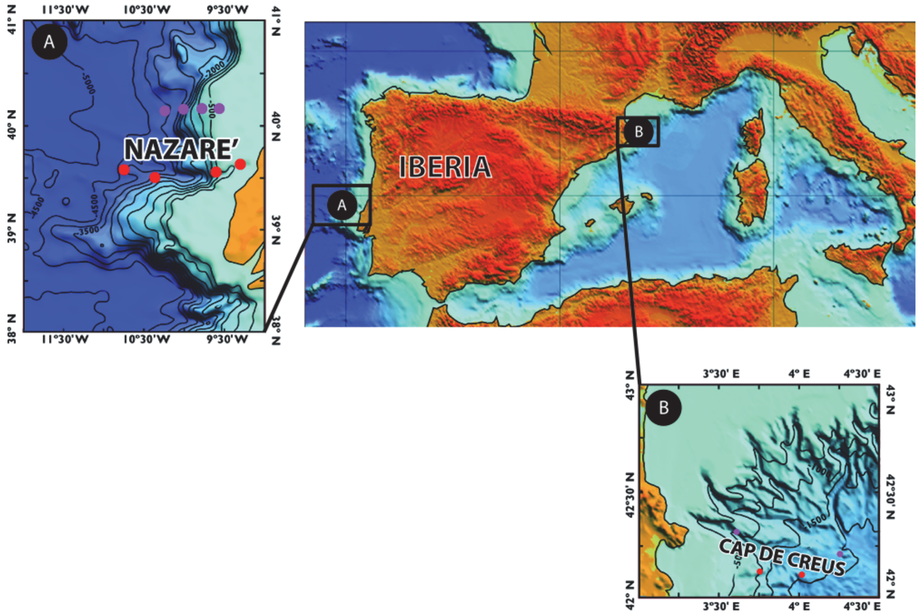

Fig. 1. Study area and sampling locations in the Portuguese **(A)** and Catalan **(B)** margins, offshore west and east Iberia, respectively.

BGD
9, 17619–17650, 2012

Trophic state of sediments from two deep continental margins

A. Dell'Anno et al.

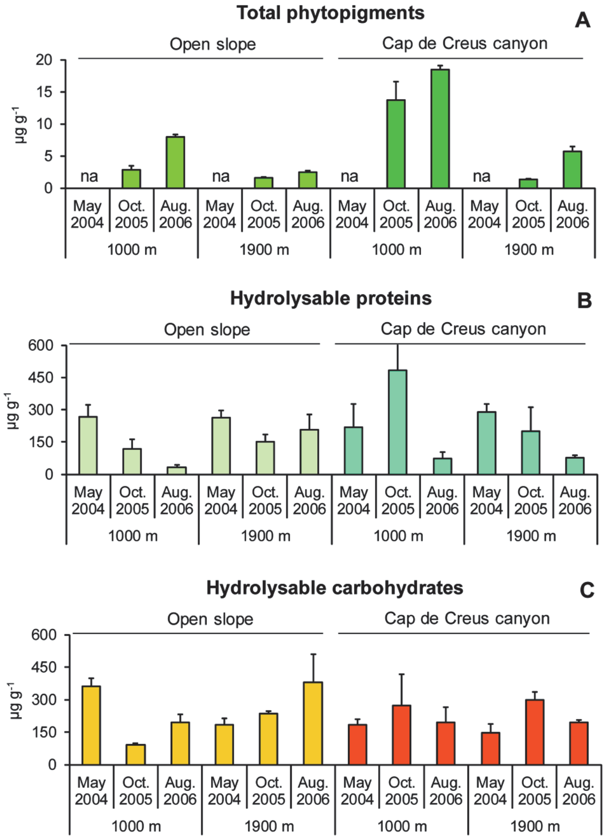

Fig. 2. Spatial distribution of **(A)** total phytopigment concentrations, **(B)** enzymatically hydrolysable protein and **(C)** carbohydrate pools in surface sediments of the Cap de Creus canyon and adjacent open slope of the Catalan margin collected in the different sampling periods. na = not available. Standard deviations are reported.

BGD
9, 17619–17650, 2012

Trophic state of sediments from two deep continental margins

A. Dell'Anno et al.

Title Page
Abstract Introduction
Conclusions References
Tables Figures
◀ ▶
Back Close
Full Screen / Esc
Printer-friendly Version
Interactive Discussion

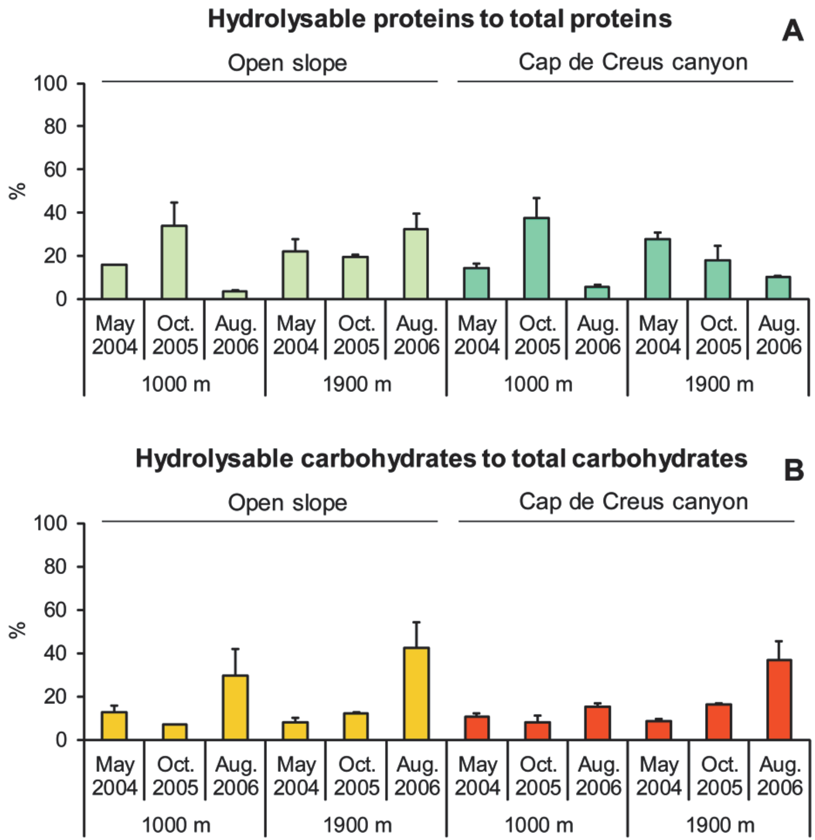

Fig. 3. Spatial patterns of the contribution of **(A)** enzymatically hydrolysable proteins and **(B)** carbohydrates to their respective total pools in surface sediments of the Cap de Creus canyon and adjacent open slope of the Catalan margin collected in the different sampling periods. Standard deviations are reported.

BGD

9, 17619–17650, 2012

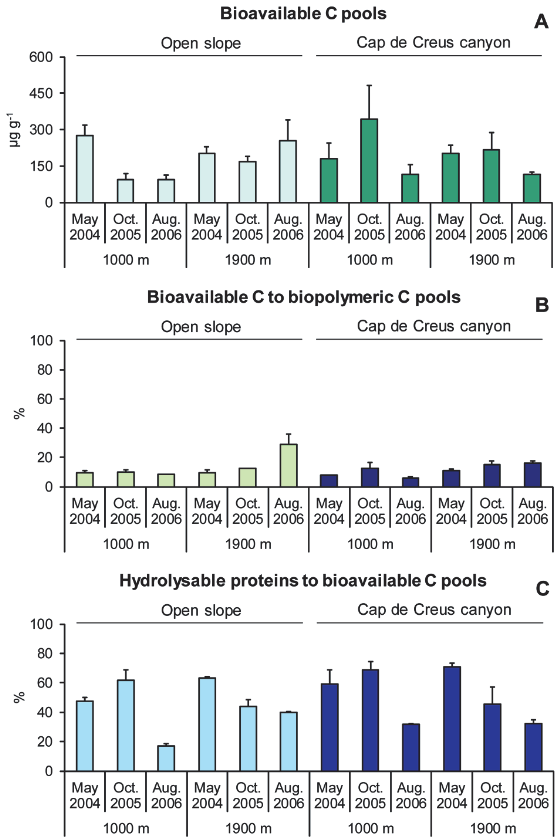

Fig. 4. Spatial distribution of **(A)** bioavailable C concentrations, **(B)** contribution of bioavailable C to biopolymeric C pools and **(C)** contribution of hydrolysable proteins (converted into C equivalents) to bioavailable C pools in surface sediments of the Cap de Creus canyon and adjacent open slope of the Catalan margin collected in the different sampling periods. Standard deviations are reported.

BGD
9, 17619–17650, 2012

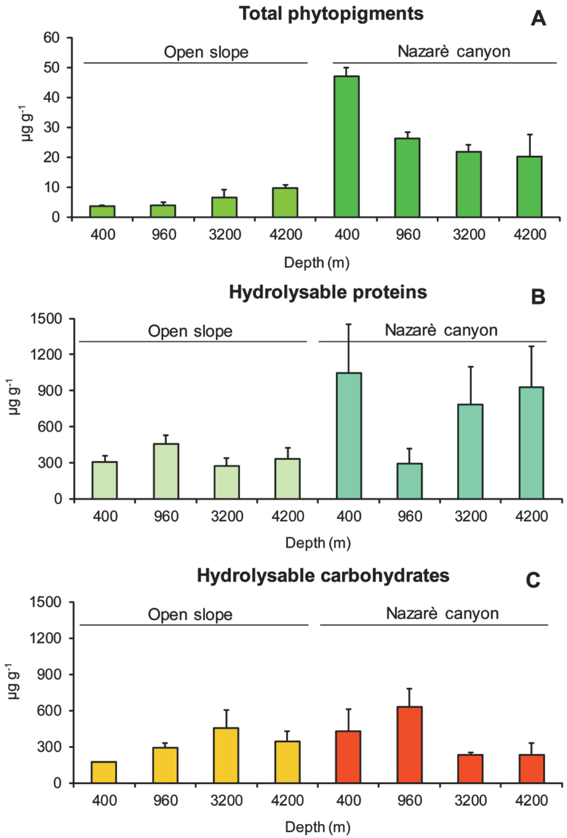

Fig. 5. Spatial distribution of **(A)** total phytopigment concentrations, **(B)** enzymatically hydrolysable protein and **(C)** carbohydrate pools in surface sediments of the Nazarè canyon and adjacent open slope of the Portuguese margin. Standard deviations are reported.

BGD
9, 17619–17650, 2012

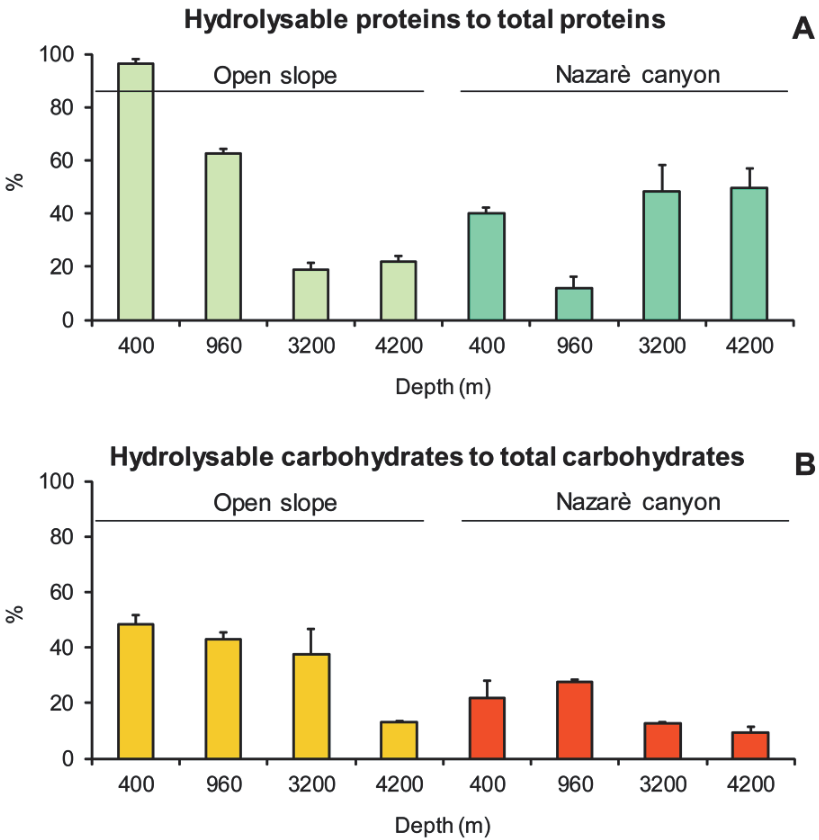

Fig. 6. Spatial patterns of the contribution of **(A)** enzymatically hydrolysable proteins and **(B)** carbohydrates to their respective total pools in surface sediments of the Nazarè canyon and adjacent open slope of the Portuguese margin. Standard deviations are reported.

BGD
9, 17619–17650, 2012

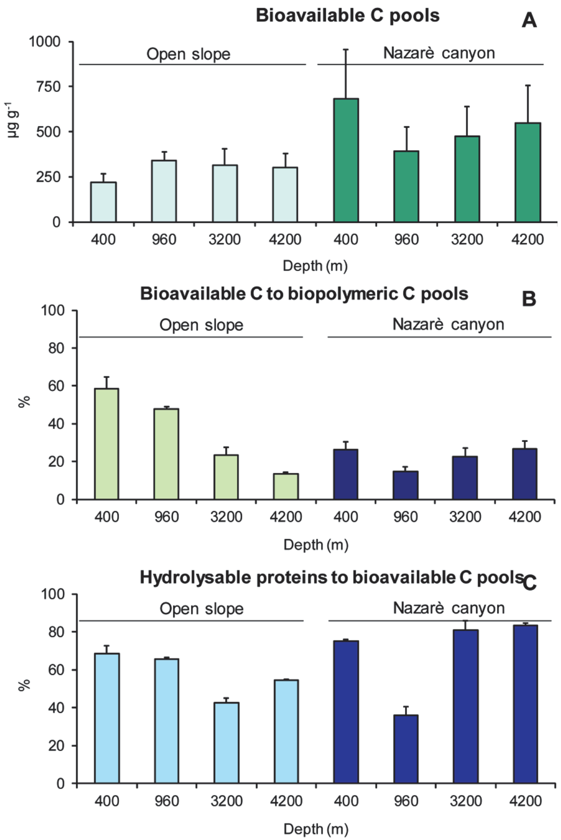

Fig. 7. Spatial distribution of **(A)** bioavailable C concentrations, **(B)** contribution of bioavailable C to biopolymeric C pools and **(C)** contribution of hydrolysable proteins (converted into C equivalents) to bioavailable C pools in surface sediments of the Nazarè canyon and adjacent open slope of the Portuguese margin. Standard deviations are reported.