



ELSEVIER

Contents lists available at ScienceDirect

## Deep-Sea Research I

journal homepage: [www.elsevier.com/locate/dsrI](http://www.elsevier.com/locate/dsrI)

## Organic matter in sediments of canyons and open slopes of the Portuguese, Catalan, Southern Adriatic and Cretan Sea margins

Antonio Pusceddu<sup>a,\*</sup>, Silvia Bianchelli<sup>a</sup>, Miquel Canals<sup>b</sup>, Anna Sanchez-Vidal<sup>b</sup>,  
Xavier Durrieu De Madron<sup>c</sup>, Serge Heussner<sup>c</sup>, Vasilios Lykousis<sup>d</sup>, Henko de Stigter<sup>e</sup>,  
Fabio Trincardi<sup>f</sup>, Roberto Danovaro<sup>a</sup>

<sup>a</sup> Dipartimento di Scienze del Mare, Università Politecnica delle Marche, Via Brecce Bianche, 60131 Ancona, Italy

<sup>b</sup> GRC Geociències Marines, Departament d'Estratigrafia, P. i Geociències Marines, Universitat de Barcelona, E-08028 Barcelona, Spain

<sup>c</sup> CEFREM, UMR 5110 CNRS-University of Perpignan, F-66860 Perpignan Cedex, France

<sup>d</sup> Hellenic Center for Marine Research, Hellinikon, Athens 16604, Greece

<sup>e</sup> Royal Netherlands Institute For Sea Research, P.O. Box 59, NL-1790 AB Den Burg, Texel, The Netherlands

<sup>f</sup> Istituto Scienze Marine, CNR, Sede di Bologna, Via P. Gobetti 101, 40129 Bologna, Italy

### ARTICLE INFO

#### Article history:

Received 6 October 2008

Received in revised form

16 November 2009

Accepted 18 November 2009

Available online 26 November 2009

#### Keywords:

Submarine canyons

Open slopes

Sediment organic matter

Trophic conditions

Mediterranean Sea

Atlantic Ocean

### ABSTRACT

We describe the quantitative and compositional (phytopigment, protein, carbohydrate and lipid) patterns of sedimentary organic matter along bathymetric gradients in seven submarine canyons and adjacent open slopes located at four European regions: one along the NE Atlantic and three along the Mediterranean continental margins. The investigated areas are distributed along a putative longitudinal gradient of decreasing primary production from the Portuguese (northeastern Atlantic Ocean), to the Catalan (western Mediterranean Sea), Southern Adriatic (central Mediterranean Sea) and Southern Cretan (eastern Mediterranean Sea) margins. Sediment concentrations of organic matter differed significantly between the Portuguese margin and the Mediterranean regions and also from one study area to the other within the Mediterranean Sea. Differences in quantity and composition of sediment organic matter between canyons and open slopes were limited and significant only in the eutrophic Portuguese margin, where the differences were as large as those observed between regions (i.e. at the mesoscale). These results suggest that the overall trophic status of deep margin sediments is controlled mostly by the primary productivity of the overlying waters rather than by the local topography. Moreover, we also report that the quantity and nutritional quality of sediment organic matter in canyons and adjacent open slopes do not show any consistent depth-related pattern. Only the Nazaré and Cascais canyons in the Portuguese margin, at depths deeper than 500 m, displayed a significant accumulation of labile organic matter. The results of our study underline the need of further investigations of deep margins through sampling strategies accounting for adequate temporal and spatial scales of variability.

© 2009 Elsevier Ltd. All rights reserved.

### 1. Introduction

Continental margins in all of the world oceans play a key role in global biogeochemical cycles (Walsh, 1991; Bauer and Druffel, 1998; Bousquet et al., 2000; Dickens, 2003; Dell'Anno and Danovaro, 2005). From the topography viewpoint continental margins are characterised by complex successions of open slopes, submarine canyons and landslide-affected areas (Weaver et al., 2004). Submarine canyons in particular are valleys deeply cut in the continental slope that may extend to the continental rise

downwards and to the continental shelf upwards. Submarine canyons dissect most of Europe's continental margins, with some of them opening their heads at short distance from the shoreline (Canals et al., 2006). The location and topography of submarine canyons make them sites of intense exchanges between the shoreline, the continental shelf and the deep continental margin. Canyons also affect local hydrodynamic conditions and often are sites of enhanced productivity (Durrieu de Madron, 1994; Monaco et al., 1999a; Mullenbach and Nittrouer, 2000; Puig et al., 2000, 2003; Rogers et al., 2003; Bosley et al., 2004; Weaver et al., 2004).

High downward mass fluxes have been reported in numerous submarine canyons worldwide (Palanques et al., 2005, 2006; Heussner et al., 2006; Canals et al., 2006, and references therein).

\* Corresponding author. Tel.: +39 071 2204747; fax: +39 071 2204650.  
E-mail address: a.pusceddu@univpm.it (A. Pusceddu).

By intercepting and trapping littoral sediment drifts, submarine canyons with their heads close to the shoreline can act as main drivers of local sediment transport and deposition, thus funnelling materials towards the adjacent deep sea (Lewis and Barnes, 1999; Schmidt et al., 2001; Flexas et al., 2002; Palanques et al., 2006).

Submarine canyons are more active in the transfer of sediment and organic matter than open slopes (Monaco et al., 1999b; Buscail and Germain, 1997; Durrieu de Madron et al., 1999; Martin et al., 2006; Epping et al., 2002; Sanchez-Vidal et al., 2008). However, along canyon and across slope the sediment transport is neither constant nor unidirectional but a pulse-like process. For example, in the Nazaré canyon off Portugal cycles of sediment resuspension and transport alternate with intervals during which the sediment accumulates on the canyon seabed (de Stigter et al., 2007). One of the most dramatic examples of pulsation processes driving large amounts of sediment and organic matter during short-lived episodes (several weeks) is the cascading of dense shelf water that makes canyons behave as flushing conduits (Canals et al., 2006, 2009; Sanchez-Vidal et al., 2008).

Submarine canyons might have a great influence on the food web and ecosystem functioning in the deep sea (Bosley et al., 2004; Skliris and Djenidi, 2006). Until now, most studies carried out on the availability as food of the organic material accumulated in submarine canyon sediments have dealt with total organic carbon and nitrogen (Buscail and Germain, 1997; Monaco et al., 1999b; Durrieu de Madron et al., 2000; Duineveld et al., 2001; Martin et al., 2006), whereas little information is available on the material's biochemical composition (Etcheber et al., 1999; Bianchelli et al., 2008).

The biopolymeric fraction of sedimentary organic C, as the sum of protein, carbohydrate and lipid carbon equivalents, has been often reported as the fraction of total organic C potentially available to benthic consumers (Danovaro et al., 2001a; Dell'Anno et al., 2002, 2003). Biopolymeric compounds are detectable down to the deepest ocean depths (Danovaro et al., 2003), thus representing more consistent tracers of the food available to the benthos than the phytopigments, which are often very low in deep-sea sediments (Danovaro et al., 2000a, 2001a). Moreover, the relative importance of the different biochemical components of biopolymeric C may provide information on the origin and fate of sediment organic matter (Fabiano et al., 1995, 2001; Pusceddu et al., 2000).

Although the inventory can locally provide estimates of the actual organic matter contents in sediments that are different from estimates obtained solely from the top of a sediment core, the analysis of the top cm has been demonstrated to represent a feasible proxy of the whole trophic status of marine sediments (Pusceddu et al., 2009a).

In the present study, we investigated the contents and the biochemical composition of organic matter in the sediments along bathymetric gradients in seven submarine canyons and adjacent open slopes located at four European regions along a putative gradient of decreasing primary production (and of organic inputs from the upper shelf): the Portuguese (northeastern Atlantic Ocean), Catalan (western Mediterranean Sea), South Adriatic (central Mediterranean Sea) and South Cretan (eastern Mediterranean Sea) margins.

To assess shifts in concentrations and biochemical composition of organic matter in the sediment of submarine canyons and adjacent open slopes and the potential effects of canyons in fuelling the adjacent deep-sea basins, we tested the following null hypotheses: (i) the content and nutritional quality of sediment organic matter in canyons and adjacent open slopes do not show any depth-related pattern; and (ii) the content and nutritional quality of organic matter in canyon sediments do not differ from

those in the sediments of the adjacent open slopes at similar depths.

We also investigated whether and to which point the general environmental setting, including variables such as water depth, latitude, longitude, bottom temperature and salinity, sediment grain size and primary production in the upper water layers can explain deep-sea sediment trophic conditions. To highlight the presence of consistent or idiosyncratic patterns among different topographic features, this investigation was done on canyon and slope sediments separately.

## 2. Materials and methods

### 2.1. Sampling

Samples from the upper 1 cm of the sediment were collected at each margin (Fig. 1), at increasing water depths along the main axis of the canyons and the adjacent open slopes as follows.

Along the Portuguese margin, sediment samples were collected with a multiple-corer in September 2006 using the R/V Pelagia from 21 stations (at depths ranging from 416 to 4987 m) located in the Nazaré and Cascais canyons and in two adjacent open slopes (hereafter, the northern Portuguese and southern Portuguese slopes). The Nazaré is a highly active canyon in terms of sediment transport, in particular during winter, whereas upwelling events may prevent sediment export during summer. Transport and rapid sediment accumulation are generally restricted to the upper and middle parts of the Nazaré canyon (Lastras et al., 2009). On the other hand, the Cascais canyon, reflecting an initial phase in submarine canyon evolution, is characterized by slope failures in its upper part (Lastras et al., 2009).

Recent studies conducted on the Catalan margin showed that the Cap de Creus canyon represents a preferential pathway for particle transport and that the main export of large amounts of water and sediment to the deep-sea environment is represented by the dense shelf water cascading repeatedly during winter periods (Canals et al., 2006; Sanchez-Vidal et al., 2008). Along the Catalan margin, sediment samples were collected with a multiple-corer in October 2005 using the R/V Universitatis from 12 stations (at depth ranging from 334 to 2342 m) located in the Cap de Creus, Lacaze-Duthiers and Sete canyons and in two adjacent open slopes (hereafter the northern Catalan and southern Catalan slopes).

Along the South Adriatic margin, sediment samples were collected with a box-corer in May 2006 using the R/V Urania from 11 stations (at depths ranging from 196 to 908 m) located within two neighbouring canyons (B and C) and the open slope (hereafter the southern Adriatic slope) between them. Canyons B and C in the South Adriatic margin play an important role in the water dynamics of the entire Adriatic basin, interacting with the Levantine Intermediate Water (LIW), the North Adriatic Deep Water (NAdDW) and the South Adriatic Deep Water (SADW) (Tesi et al., 2008). These canyons in the South Adriatic margin are efficient conduits in delivering suspended sediment from the continental shelf to the deep southern Adriatic basin, with maximum mass fluxes during spring periods (Tesi et al., 2008).

Along the South Cretan margin, sediment samples were collected with a box-corer in June 2006 using the R/V Aegaeo from 11 stations (at depths ranging from 216 to 3600 m) located in the Samaria canyon and two adjacent open slopes (hereafter the western Cretan and eastern Cretan slopes). In the South Cretan margin there is no evidence of preferential transport of particulate matter along the canyons axes and, at the time of sampling, suspended particle distribution along the canyon axes

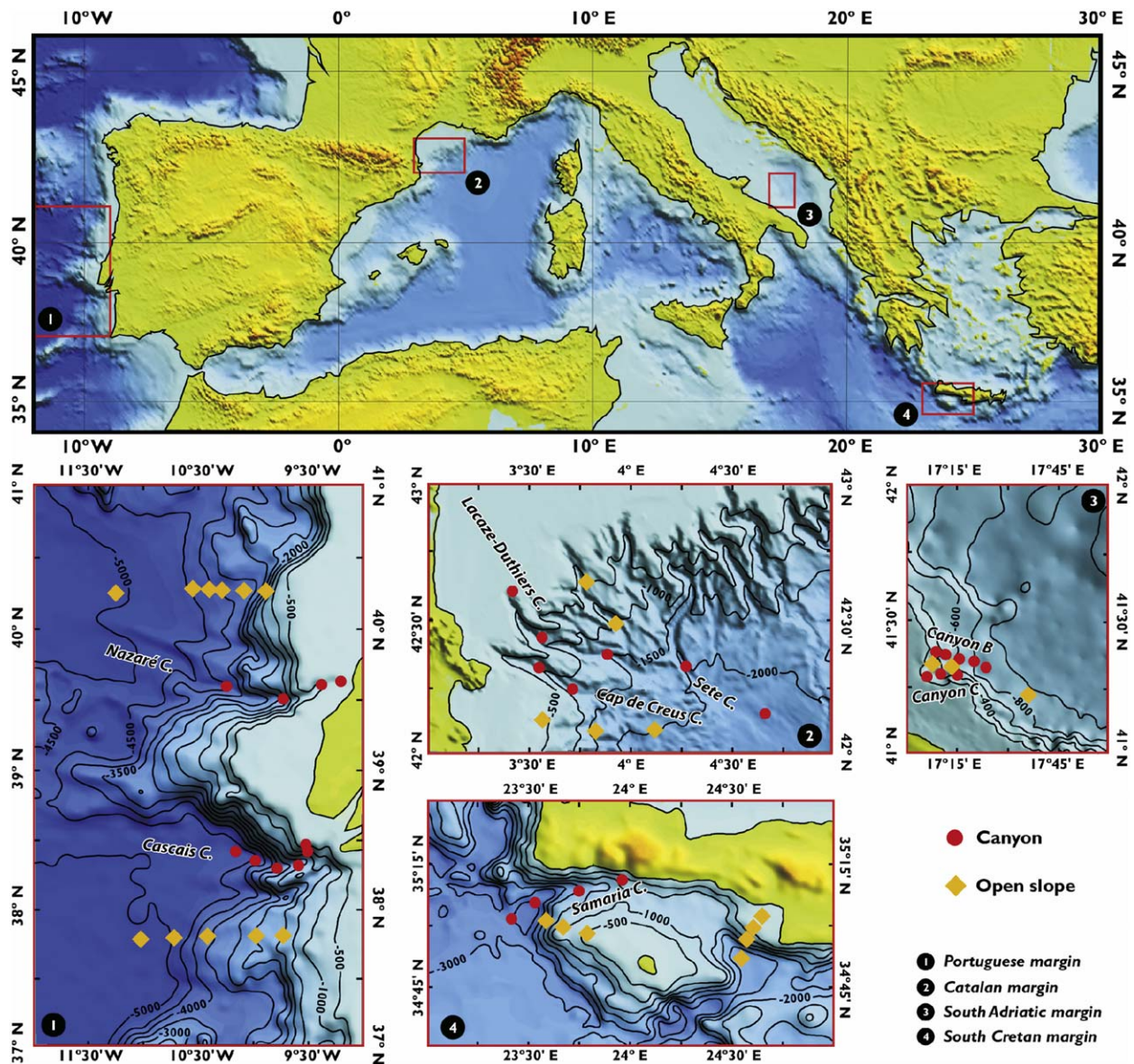


Fig. 1. Sampling area and station locations.

and the open slopes did not show particular patterns (Lykousis pers comm). It is, however, likely that the Samaria canyon could be episodically characterised by important downwelling processes during intense rainfall events.

Near-bottom temperature and salinity measurements were collected in parallel to sediment coring by means of a Seabird 911 CTD probe.

The location and depth of all of the sampled stations are reported in Table 1.

## 2.2. Sediment grain size

Aliquots of sediment were treated with 10% hydrogen peroxide in a large beaker for 24–48 h and dried in the oven at 60 °C for an additional 24 h. The sediment was then sieved through a 63- $\mu$ m sieve and the two fractions (sands > 63  $\mu$ m, and mud < 63  $\mu$ m) weighed ( $\pm 0.1$  mg) and expressed as percentage of the initial total dry weight.

## 2.3. Phytopigment contents

Chlorophyll-*a* and phaeopigment analyses were carried out according to Lorenzen and Jeffrey (1980). For all of the stations, pigments were extracted (12 h at 4 °C in the dark) from triplicate superficial (0–1 cm) sediment samples (about 1 g) obtained from independent deployments of the multiple- or box-corer, using 3–5 ml of 90% acetone as the extractant. Extracts were analysed fluorometrically to estimate chlorophyll-*a*, and, after acidification with 200  $\mu$ l 0.1 N HCl, to estimate phaeopigments. Different methods for assessing chlorophyll-*a* concentrations in marine sediments can provide different under- or overestimates (Pinckney et al., 1994), also because of the relative importance of the chlorophyll degradation products (Szymczak-Żyła and Kowalewska, 2007). Since chlorophyll degradation products are typically dominant in deep-sea sediments, as being mostly associated with degraded algal material that has settled from the upper water column layers, the use of chlorophyll-*a* estimates based on the fluorometric method could be useful only for comparisons, but not if actual concentrations are important (Pinckney et al., 1994).



For this reason, we avoided use of the fluorometric chlorophyll-*a* estimates as the unique tracer of organic C associated with algal material and, instead, summed chlorophyll-*a* and phaeopigment concentrations (i.e. total phytopigments). Concentrations of total phytopigments, once converted into C equivalents using 40 as a conversion factor (Pusceddu et al., 1999), are reported in  $\mu\text{g C g}^{-1}$ .

#### 2.4. Quantity and biochemical composition of sediment organic matter

Protein, carbohydrate and lipid contents were analysed spectrophotometrically according to Pusceddu et al. (2004) 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 superficial (0–1 cm) sediment samples (about 0.5 g) obtained from independent deployments of the multiple- or box-corer. Carbohydrate, protein and lipid sediment contents were converted into C equivalents using the conversion factors 0.40, 0.49 and 0.75  $\text{mg C mg}^{-1}$ , respectively, and their sum defined as the biopolymeric carbon (Fabiano et al., 1995).

For the purposes of the present study, we chose the contributions of phytopigment and protein to biopolymeric C concentrations and the values of the protein to carbohydrate ratio as descriptors of the aging and nutritional quality of sediment organic matter (Pusceddu et al., 2000, 2009a). The percentage contribution of total phytopigments to biopolymeric C is an estimate of the freshness of the organic material deposited in the sediment: since photosynthetic pigments and their degradation products are assumed to be labile compounds in a trophodynamic perspective, the lower their contribution to sediment organic C the more aged the organic material. Moreover, since the percentage fraction of organic C associated with phytopigments is also typically associated with a higher fraction of enzymatically digestible (i.e. promptly available for heterotrophs) compounds (Pusceddu et al., 2003), higher values of this percentage will also be indicative of a comparatively higher nutritional quality (Dell'Anno et al., 2002). Since N is the most limiting factor for heterotrophic nutrition and proteins, which are degraded at faster rates than carbohydrates, and are N-rich products, the protein to biopolymeric C and the protein to carbohydrate ratios are indicative of both the aging and the nutritional value of the organic matter (Danovaro et al., 1993, 2001b; Dell'Anno et al., 2002; Tselepidis et al., 2000; Pusceddu et al. 2009a).

#### 2.5. Statistical analyses

To test for bathymetric changes in the concentrations and biochemical composition of organic matter in canyon and open slope sediments, one-way analysis of variance (ANOVA) was carried out for all of the measured variables separately for all of the canyons and open slopes, using stations (sampling depths) as fixed factors. When significant differences were encountered, a Student–Newman–Keuls (SNK) post-hoc comparison test (at  $\alpha=0.05$ ) was also carried out to ascertain in which of the investigated transects concentrations significantly decreased with water depth. Before the analyses, 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 us to obtain homogeneous variances, a more conservative level of significance was considered (Underwood, 1991). When significant differences were encountered, a SNK post-hoc comparison test (at  $\alpha=0.05$ ) was also

carried out. All ANOVA and SNK tests were conducted using the GMAV 5.0 software (University of Sydney, Australia).

Distance-based permutational multivariate analyses of variance (PERMANOVA; Anderson, 2001; McArdle and Anderson, 2001) were used to test for differences in quantity and biochemical composition of organic matter in sediments of canyons and open slopes with increasing water depth (including in the analysis only stations located at similar depths). The PERMANOVA test is an analogue of the multivariate analysis of variance (MANOVA), which, however, is too stringent in its assumptions for most ecological multivariate data sets (Anderson, 2001). Non-parametric methods based on permutation tests, such as the one performed by the PERMANOVA tool, are preferable, since they allow partition of the variability in the data according to a complex design or model and to base the analysis on a multivariate distance measure that is reasonable for ecological data sets (McArdle and Anderson, 2001). The design included two factors: the topographic feature (*T*, 3–4 levels, fixed) and the water depth (*D*, two levels, random and nested in *T*), with  $n=3$  for the combination of factors. The analysis was based on Euclidean distances of previously normalized data, using 4999 random permutations of the appropriate units (Anderson and ter Braak, 2003). The analysis was run using the FORTRAN-written PERMANOVA.exe program (Anderson, 2005). The pseudo-multivariate variance components for each term in the model were calculated using direct multivariate analogues to the univariate ANOVA estimators (e.g. Searle et al., 1992).

ANOSIM analysis was performed to test the presence of statistical differences between *a priori* grouped transects or grouped depths. When significant differences were observed, non-metric multidimensional scaling (nMDS) ordinations were carried out to visualize similarities at different spatial scales: i.e. (i) area (Atlantic, western, central and eastern Mediterranean) and (ii) topographic feature (canyons vs. slope) at similar depths (i.e. 500, 1000 and 2000 m water depth). Separate ranked matrices of Euclidean distance similarity were based on (i) phytopigment, protein, carbohydrate and lipid concentrations for the organic matter quantity (Dell'Anno et al., 2002) and (ii) on the phytopigment and protein contributions to biopolymeric C and the values of the protein to carbohydrate ratio (Pusceddu et al., 2000) for the organic matter nutritional quality. nMDS plots are produced in order to represent the samples as points in low dimensional space (2D in the present study), so that the relative distances apart of all points are in the same rank order as the relative dissimilarities of the samples (here calculated as Bray Curtis coefficients): points close together represent very similar samples, and points far apart represent very different samples. Therefore, nMDS plots have no axis scales or meaningful absolute units for the axes, the relative distances between plotted points being the only meaningful result (Clarke and Gorley, 2001). Stress values indicate how faithfully the multivariate relationships are represented in the 2D ordination plot: the lower the stress value the more representative the plot (Clarke and Gorley, 2001).

SIMPER analysis with a cut of 90% (i.e. by removing variables cumulatively explaining less than 10% of the variance) was then applied to identify which among the investigated variables contributed most to the similarities between sites. nMDS, SIMPER and ANOSIM analyses were performed using PRIMER 5.0 (Plymouth Marine Laboratory, UK; Clarke, 1993).

To assess whether and how much latitude, longitude, temperature and sediment grain size and primary productivity at the sea surface explained changes in concentration and nutritional quality of superficial sediment organic matter in canyons and open slopes at different spatial scales (i.e. area, canyon and slopes within the same area) non-parametric multivariate multiple regression analyses that were based on Euclidean distances

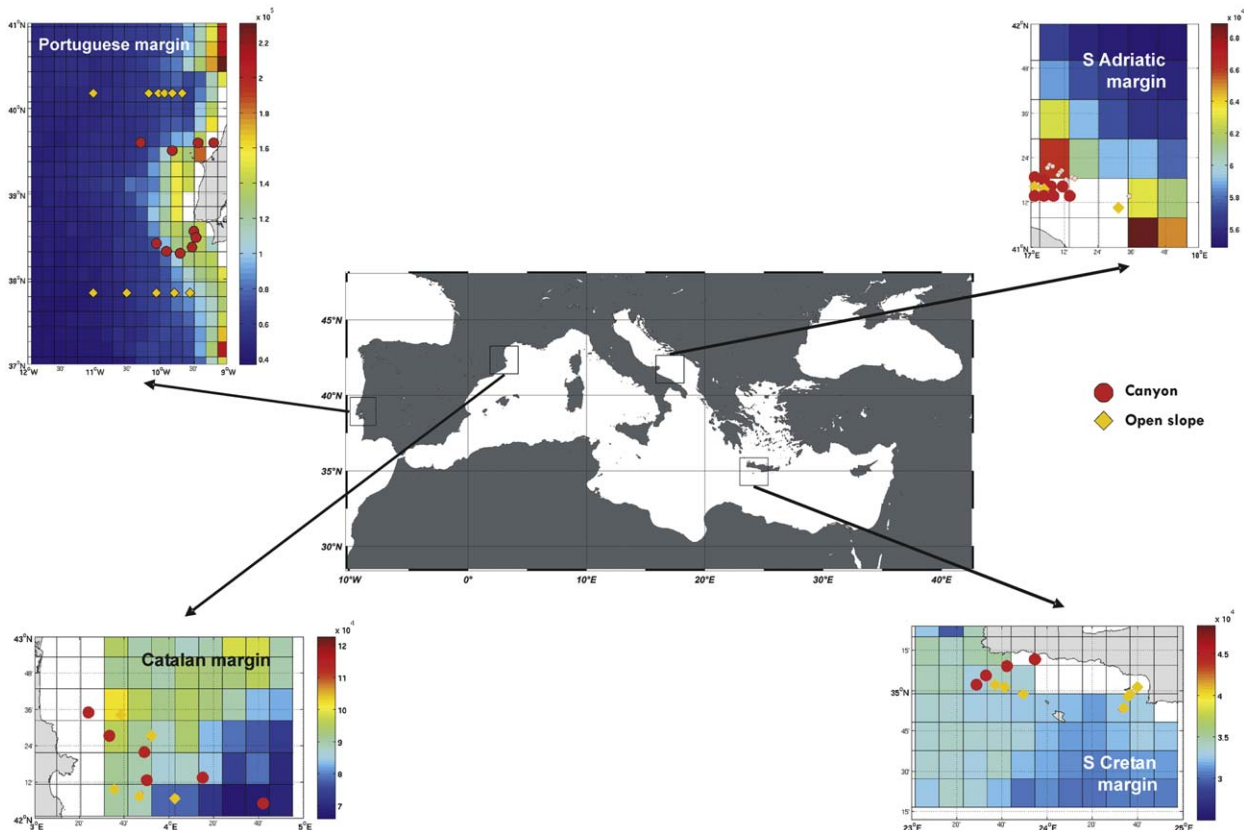


Fig. 2. Primary productivity spatial patterns in the four study areas.

were carried out using the routine DISTLM forward (McArdle and Anderson, 2001). The forward selection of the predictor variables was carried out with tests by permutation.  $P$  values were obtained using 4999 permutations of raw data for the marginal tests (tests of individual variables), while for all of the conditional tests, the routine uses 4999 permutations of residuals under a reduced model.

Data of primary productivity in the investigated areas were extracted from the Ocean Productivity database (<http://www.science.oregonstate.edu/ocean.productivity/index.php>). In particular, we used data of primary productivity estimated by means of the vertically generalized production model (VGPM; Behrenfeld and Falkowski, 1997) as the standard algorithm. For all of the investigated areas the multivariate multiple regression analysis included estimated primary productivity data obtained as monthly averaged values, corresponding to the month of sediment sample collection. Spatial distribution of primary productivity in the areas under scrutiny is illustrated in Fig. 2.

Relationships between the concentrations of biopolymeric C and the different descriptors of nutritional quality and organic matter aging were assessed by a Spearman rank correlation analysis.

### 3. Results

The bottom temperature and salinity values, grain size features of the sediment and the phytopigment, protein, carbohydrate, lipid and biopolymeric C concentrations in the sediment of all of the stations are reported in Table 1.

The total phytopigment concentrations ranged from  $0.50 \pm 0.05$  in the western Cretan slope at 1081 m depth to  $55 \pm 13 \mu\text{g g}^{-1}$  in the Cascais canyon at 1021 m water depth.

The protein concentrations ranged from  $0.14 \pm 0.02$  in canyon C at 341 m depth to  $3.67 \pm 0.29 \text{ mg g}^{-1}$  in the Lacaze-Duthiers canyon at 434 m depth. The carbohydrate concentrations ranged from  $0.36 \pm 0.03$  in the northern Portuguese open slope at 416 m depth to  $4.9 \pm 0.5 \text{ mg g}^{-1}$  in the northern Catalan open slope at 1022 m depth. The lipid concentrations ranged from  $0.02 \pm 0.01$  to  $1.4 \pm 0.4 \text{ mg g}^{-1}$ , in canyon C at 341 m and the southern Catalan open slope at 398 m water depth, respectively. The total concentration of biopolymeric C ranged from  $0.32 \pm 0.06$  to  $3.8 \pm 0.6 \text{ mg g}^{-1}$  in the Adriatic canyon C at 341 m depth and in the Lacaze-Duthiers canyon at 434 m water depth, respectively.

#### 3.1. Bathymetric gradients of sediment organic matter concentrations

The one-way ANOVA carried out to assess water depth-related patterns in sediment organic matter concentrations separately for all of the study sites revealed that changes occurred at all of the four study areas, but also showed that those changes were not consistent for all the investigated variables (Table 2).

Protein sediment content displayed significant differences between sampling depths at some of the study sites but not in the Nazaré canyon, the southern Portuguese slope, the northern Catalan slope, the canyon B in the Adriatic Sea and in the eastern Cretan slope (Fig. 3a). Carbohydrate concentrations displayed significant differences between sampling depths at all sites, with the exception of the Nazaré canyon and all of the sites in the South Cretan margin (Fig. 3b). Lipid contents in superficial sediments displayed significant differences between sampling depths in all of the investigated transects (Fig. 3c).

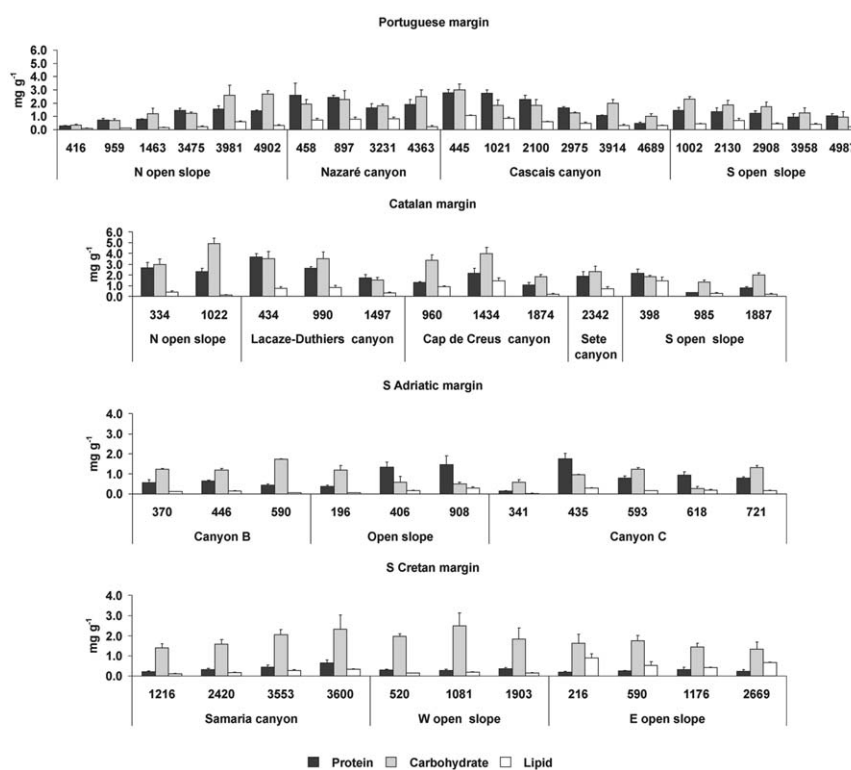
Total phytopigment concentrations displayed significant differences between sampling depths at all transects, except in the

**Table 2**

Output of the one-way ANOVA analysis and the SNK tests carried out in all study areas to ascertain differences in sediment organic matter concentration with increasing water column depth.

| Stations location           | Phytopigments |     |     | Proteins |     |     | Carbohydrates |     |     | Lipids |     |     | Biopolymeric C |     |     |
|-----------------------------|---------------|-----|-----|----------|-----|-----|---------------|-----|-----|--------|-----|-----|----------------|-----|-----|
|                             | F             | P   | SNK | F        | P   | SNK | F             | P   | SNK | F      | P   | SNK | F              | P   | SNK |
| N Portuguese slope          | 8.79          | *** | +   | 38.13    | *** | +   | 20.73         | *** | +   | 53.56  | *** | +   | 28.04          | *** | +   |
| Nazaré canyon               | 31.41         | *** | –   | 2.23     | ns  | ns  | 1.59          | ns  | ns  | 15.80  | **  | –   | 1.29           | ns  | ns  |
| Cascais canyon              | 26.72         | *** | –   | 63.32    | *** | –   | 12.48         | *** | –   | 41.78  | *** | –   | 29.49          | *** | –   |
| S Portuguese slope          | 16.19         | *** | –   | 2.69     | ns  | ns  | 7.40          | **  | –   | 10.33  | **  | –   | 5.28           | *   | –   |
| N Catalan slope             | 0.74          | ns  | ns  | 1.17     | ns  | ns  | 20.53         | *   | +   | 16.24  | *   | –   | 1.17           | ns  | ns  |
| Lacaze-Duthiers/Sete canyon | 23.60         | *** | –   | 24.45    | *** | –   | 10.50         | **  | –   | 5.53   | *   | –   | 11.67          | **  | –   |
| Cap de Creus/Sete canyon    | 50.73         | *** | –   | 6.05     | *   | –   | 12.25         | **  | –   | 24.22  | *** | –   | 11.28          | **  | –   |
| S Catalan slope             | 398.49        | *** | –   | 43.12    | *** | –   | 10.64         | *   | –   | 28.92  | *** | –   | 28.39          | *** | –   |
| Canyon B                    | 9.55          | *   | –   | 4.63     | ns  | ns  | 87.84         | *** | +   | 12.83  | **  | –   | 1.09           | ns  | ns  |
| S Adriatic slope            | 105.68        | *** | +   | 11.11    | **  | +   | 8.23          | *   | –   | 20.67  | **  | +   | 2.48           | ns  | ns  |
| Canyon C                    | 116.56        | *** | –   | 40.49    | *** | –   | 67.72         | *** | +   | 57.16  | *** | –   | 37.59          | *** | –   |
| W Cretan slope              | 9.79          | **  | –   | 12.19    | **  | +   | 0.92          | ns  | ns  | 56.11  | *** | +   | 1.99           | ns  | ns  |
| Samaria canyon              | 3.41          | ns  | ns  | 11.28    | **  | +   | 3.55          | ns  | ns  | 39.19  | *** | +   | 6.84           | *   | +   |
| E Cretan slope              | 24.10         | *** | –   | 1.02     | ns  | ns  | 1.00          | ns  | ns  | 6.81   | *   | –   | 1.24           | ns  | ns  |

F=ANOVA F statistic, P=probability level (\*\*\*=P<0.001; \*\*=P<0.01; \*=P<0.05; ns=not significant), SNK=output of the Student–Newman–Kuels post-hoc test: + indicates significant increasing concentrations with increasing water column depth, – indicates significant decreasing concentrations with increasing water column depth and ns indicates not significant changes with water depth).

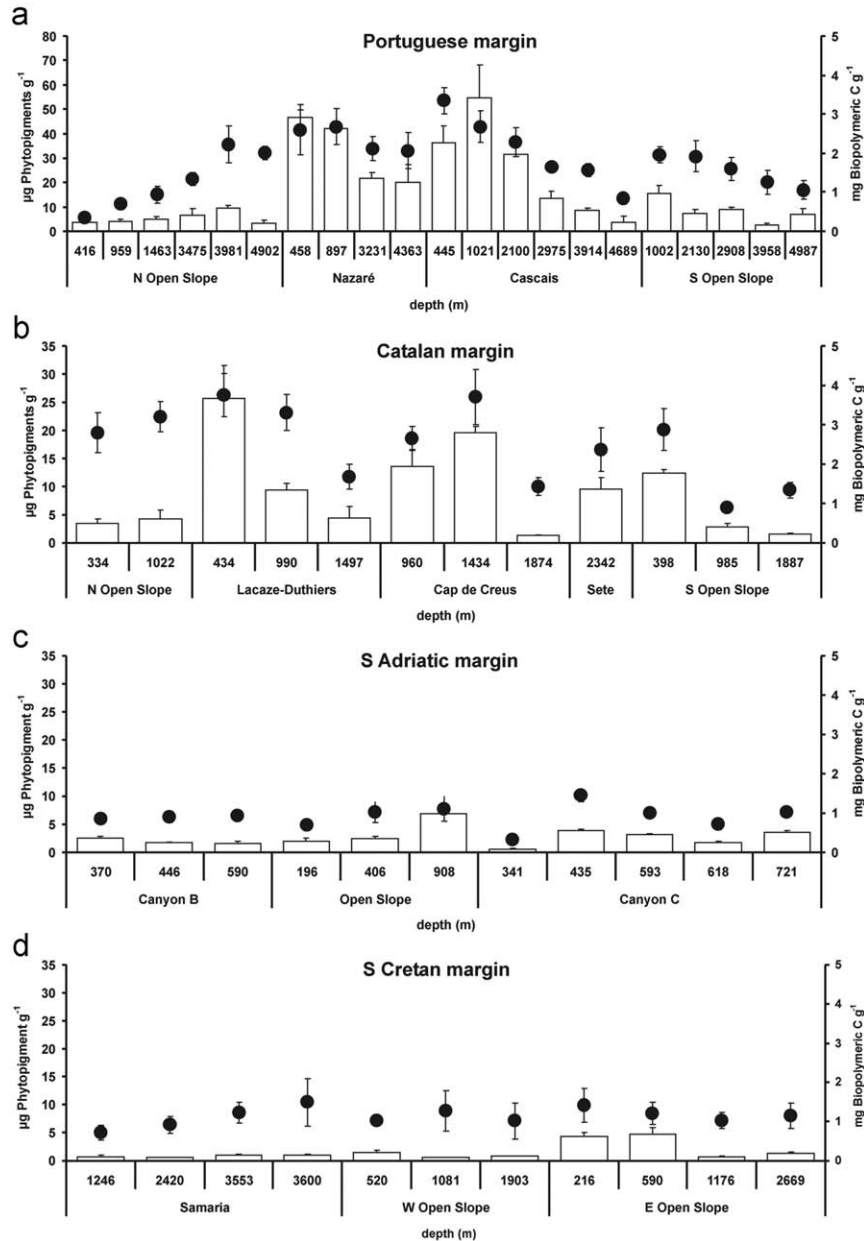


**Fig. 3.** Protein, carbohydrate and lipid contents in the sediment of all of the 55 stations along the Portuguese, Catalan, South Adriatic and South Cretan margins. Illustrated are values ( $\pm$  standard deviation of  $n=3$  replicates) from the four investigated areas, divided by open slope and canyon settings and according to the increasing depth (m) of the different sampling stations.

northern Catalan slope and the Samaria canyon (Fig. 4). Biopolymeric C concentrations displayed significant differences between sampling depths at all sites, except in the Nazaré canyon and northern Catalan slope, canyon B and open slope in the South Adriatic margin, and in the open slopes in the South Cretan margin (Fig. 4).

The results of the SNK test (Table 2) revealed also that the observed patterns with water depth were not consistent in all

transects, being characterised by increasing concentrations with water depth at some places (e.g. South Adriatic canyon B, northern Portuguese slope), by decreasing concentrations in other locations (e.g. Nazaré and Lacaze-Duthiers canyons, southern Catalan, South Adriatic and eastern Cretan slopes), and by intermediate depth peaks in the remaining sites (e.g. Cascais canyon, Cap de Creus canyon, South Adriatic canyon C, southern Portuguese and western Cretan slopes).



**Fig. 4.** Phytopigment and biopolymeric C contents in the sediment of all of the 55 stations along the Portuguese, Catalan, South Adriatic and South Cretan margins. Illustrated are values ( $\pm$  standard deviation of  $n=3$  replicates) from the four investigated areas, divided by open slope and canyon settings and according to the increasing depth (m) of the different sampling stations.

### 3.2. Differences in benthic trophic conditions between areas, topographic features and depths

The results of the PERMANOVA tests, carried out separately for each area on the quantity and nutritional quality and aging of organic matter, showed that the variability in benthic trophic conditions in all areas was explained mostly by water depth, whereas topography (canyon vs. open slope) did not have significant effects (Table 3). A west-to-east gradient in organic matter concentrations from the Portuguese to the Cretan margin was revealed by the ANOSIM tests that were consistent for the whole data set and similar water depths. As a consequence, the nMDS ordination plot based on the quantity of organic matter in the

sediment revealed that the geographical location of the study areas was of some importance (Fig. 5). This plot shows that differences between sampling areas were indeed larger than those between data points grouped according to the different topographic setting in each area. The SIMPER analysis revealed that the differences between the four study areas corresponded to differences in the total phytopigment and carbohydrate concentrations (Table 4). The nMDS ordinations carried out using qualitative attributes of the sediment organic matter (Fig. 6) revealed, indeed, that only stations located at 500 and 1000-m depth in the Portuguese canyons were characterised by significantly different qualitative attributes (i.e. significantly higher concentrations of phytopigments) of organic matter (ANOSIM,  $p < 0.01$ ). However, it

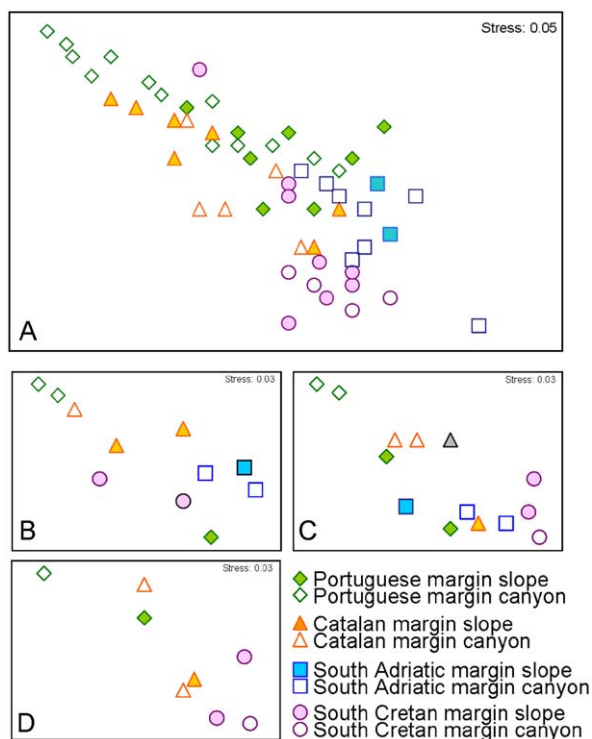


**Table 3**

Results of the PERMANOVA carried out to ascertain multivariate differences in organic matter quantity and nutritional quality between canyons and open slope within each investigated area and between depths within each topographic feature.

| Source                         | Portuguese margin       |         |       |     |                                    |      |       |     |
|--------------------------------|-------------------------|---------|-------|-----|------------------------------------|------|-------|-----|
|                                | Organic matter quantity |         |       |     | Organic matter nutritional quality |      |       |     |
|                                | df                      | MS      | F     | P   | df                                 | MS   | F     | P   |
| Canyon vs. slope               | 1                       | 1627.05 | 1.65  | ns  | 1                                  | 0.36 | 1.91  | ns  |
| Depth within canyon and slopes | 4                       | 983.63  | 29.31 | *** | 4                                  | 0.19 | 64.63 | *** |
| Residual                       | 12                      | 33.56   |       |     | 12                                 | 0.00 |       |     |
| Total                          | 17                      |         |       |     | 17                                 |      |       |     |
| <b>Catalan margin</b>          |                         |         |       |     |                                    |      |       |     |
| Canyon vs. slope               | 2                       | 157.93  | 0.62  | ns  | 2                                  | 0.66 | 2.02  | ns  |
| Depth within canyon and slopes | 6                       | 255.42  | 42.42 | *** | 6                                  | 0.33 | 50.62 | *** |
| Residual                       | 18                      | 6.02    |       |     | 18                                 | 0.01 |       |     |
| Total                          | 26                      |         |       |     | 26                                 |      |       |     |
| <b>S Adriatic margin</b>       |                         |         |       |     |                                    |      |       |     |
| Canyon vs. slope               | 2                       | 10.97   | 0.92  | ns  | 2                                  | 5.44 | 1.94  | ns  |
| Depth within canyon and slopes | 6                       | 11.94   | 56.98 | *** | 6                                  | 2.80 | 18.06 | *** |
| Residual                       | 18                      | 0.21    |       |     | 18                                 | 0.15 |       |     |
| Total                          | 26                      |         |       |     | 26                                 |      |       |     |
| <b>S Cretan margin</b>         |                         |         |       |     |                                    |      |       |     |
| Canyon vs. slope               | 2                       | 7.56    | 1.35  | ns  | 2                                  | 0.01 | 1.03  | ns  |
| Depth within canyon and slopes | 6                       | 5.59    | 12.91 | *** | 6                                  | 0.01 | 10.77 | *** |
| Residual                       | 18                      | 0.43    |       |     | 18                                 | 0.00 |       |     |
| Total                          | 26                      |         |       |     | 26                                 |      |       |     |

df=degree of freedom, MS=mean square, F=F statistic, P=probability level (\*\*\*=P < 0.001; ns=not significant).



**Fig. 5.** nMDS ordination plots based on organic matter sedimentary contents showing the similarity among the different topographic features and different areas. Illustrated are regional patterns irrespective of depth (A), at 500 (B), 1000 (C) and 2000 (D) m depth. In panel (A) the arrows and percentage numbers highlight the differences between the areas, calculated after the SIMPER analysis.

is noticeable that in the nMDS plot from which the data from the Portuguese canyons were removed all other stations were highly interspersed (Fig. 6A).

All of the descriptors of nutritional quality of sediment organic matter were significantly correlated with each other and were significantly correlated with the biopolymeric C sediment contents (Fig. 7).

### 3.3. Relationships between benthic trophic conditions and environmental constraints

The results of the multivariate multiple regression analyses carried out using the concentrations of organic matter in the sediment from all of the study areas and on the different topographic features irrespective of the area revealed that most of the variance in the quantitative trophic conditions of the sediments could be explained by a combination of primary productivity in the superficial waters, bottom temperature and salinity (Table 5). On the other hand, water depth had significant effects on the concentrations of organic matter only within the Portuguese, Catalan and South Cretan canyons, when analysed separately (data not shown). The same analysis carried out separately for each area showed that different sets of environmental variables were responsible for most of the variance of the trophic conditions and that, locally, primary productivity at the sea surface did not explain significant proportions of the benthic trophic condition variance (Table 6).

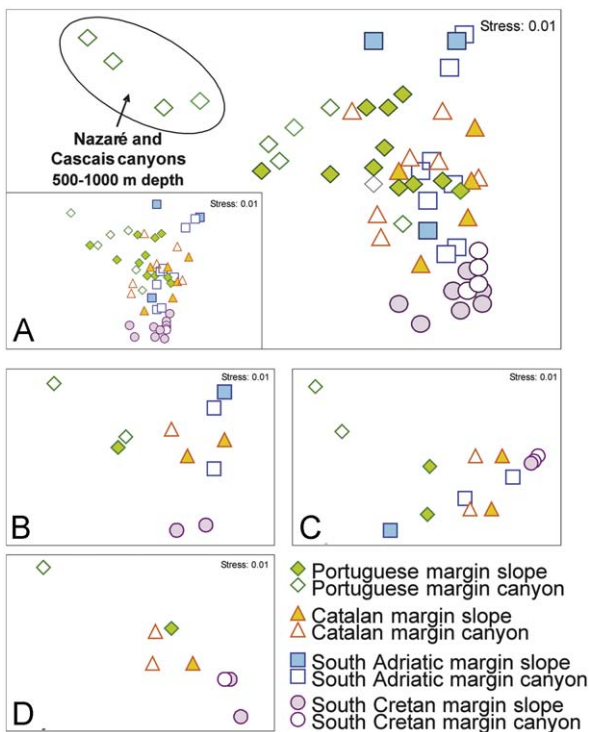
The multiple regression analysis carried out on the qualitative descriptors of sedimentary organic matter (i.e. phytopigment and protein contributions to biopolymeric C and value of the protein to carbohydrate ratio) illustrated that, at the largest spatial scale (i.e. including all the areas together), the nutritional quality of sedimentary organic matter is related mostly to the thermohaline conditions at the sea bottom and, to a lesser extent, to the upper water column primary production (Table 7A). The analyses performed on the different topographic features separately (i.e. canyons and slopes) indicated that within canyons (pooled altogether) most of the variance of the nutritional quality of

**Table 4**

Dissimilarity in sediment organic matter contents between the different areas investigated and the variables responsible for the estimated differences.

|                                  | ANOSIM |     | SIMPER            |                       |                        |                                   |
|----------------------------------|--------|-----|-------------------|-----------------------|------------------------|-----------------------------------|
|                                  | R      | P   | Dissimilarity (%) | Explanatory variable  | Explained variance (%) | Cumulative explained variance (%) |
| <b>Portuguese vs. Catalan</b>    | 0.06   | *   | 42.61             | <b>Phytopigments</b>  | 70.81                  | 70.82                             |
|                                  |        |     |                   | <b>Carbohydrates</b>  | 10.22                  | 81.03                             |
|                                  |        |     |                   | <b>Biopolymeric C</b> | 8.83                   | 89.83                             |
|                                  |        |     |                   | <b>Proteins</b>       | 7.41                   | 97.15                             |
| <b>Portuguese vs. S Adriatic</b> | 0.29   | *** | 51.42             | <b>Phytopigments</b>  | 75.83                  | 75.84                             |
|                                  |        |     |                   | <b>Carbohydrates</b>  | 7.82                   | 83.63                             |
|                                  |        |     |                   | <b>Biopolymeric C</b> | 7.31                   | 90.92                             |
| <b>Portuguese vs. S Cretan</b>   | 0.41   | *** | 56.23             | <b>Phytopigments</b>  | 77.11                  | 77.11                             |
|                                  |        |     |                   | <b>Proteins</b>       | 7.71                   | 84.83                             |
|                                  |        |     |                   | <b>Carbohydrates</b>  | 6.93                   | 91.73                             |
| <b>Catalan vs. S Adriatic</b>    | 0.39   | *** | 48.23             | <b>Phytopigments</b>  | 52.74                  | 52.74                             |
|                                  |        |     |                   | <b>Carbohydrates</b>  | 17.04                  | 69.75                             |
|                                  |        |     |                   | <b>Biopolymeric C</b> | 14.62                  | 84.33                             |
|                                  |        |     |                   | <b>Proteins</b>       | 11.65                  | 95.92                             |
| <b>Catalan vs. S Cretan</b>      | 0.39   | *** | 49.53             | <b>Phytopigments</b>  | 59.24                  | 59.22                             |
|                                  |        |     |                   | <b>Proteins</b>       | 13.93                  | 73.12                             |
|                                  |        |     |                   | <b>Biopolymeric C</b> | 12.31                  | 85.43                             |
|                                  |        |     |                   | <b>Carbohydrates</b>  | 10.92                  | 96.32                             |
| <b>S Adriatic vs. S Cretan</b>   | 0.32   | *** | 39.72             | <b>Phytopigments</b>  | 52.74                  | 52.71                             |
|                                  |        |     |                   | <b>Carbohydrates</b>  | 20.12                  | 72.82                             |
|                                  |        |     |                   | <b>Proteins</b>       | 12.11                  | 84.91                             |
|                                  |        |     |                   | <b>Biopolymeric C</b> | 9.84                   | 94.71                             |

Reported are the outputs of the ANOSIM and SIMPER analyses. R is the sample statistic (global R) and P is the probability level (\*\*\*=P < 0.001; \*=P < 0.05).



**Fig. 6.** nMDS ordination plot based on organic matter sediment bioavailability showing the similarity among the different topographic features and different areas. Illustrated are regional patterns irrespective of depth (A; the small left panel illustrates the nMDS output after the removal of data from stations in the Portuguese canyons at 500 and 1000 m depth), at 500 (B), 1000 (C) and 2000 (D) m depth.

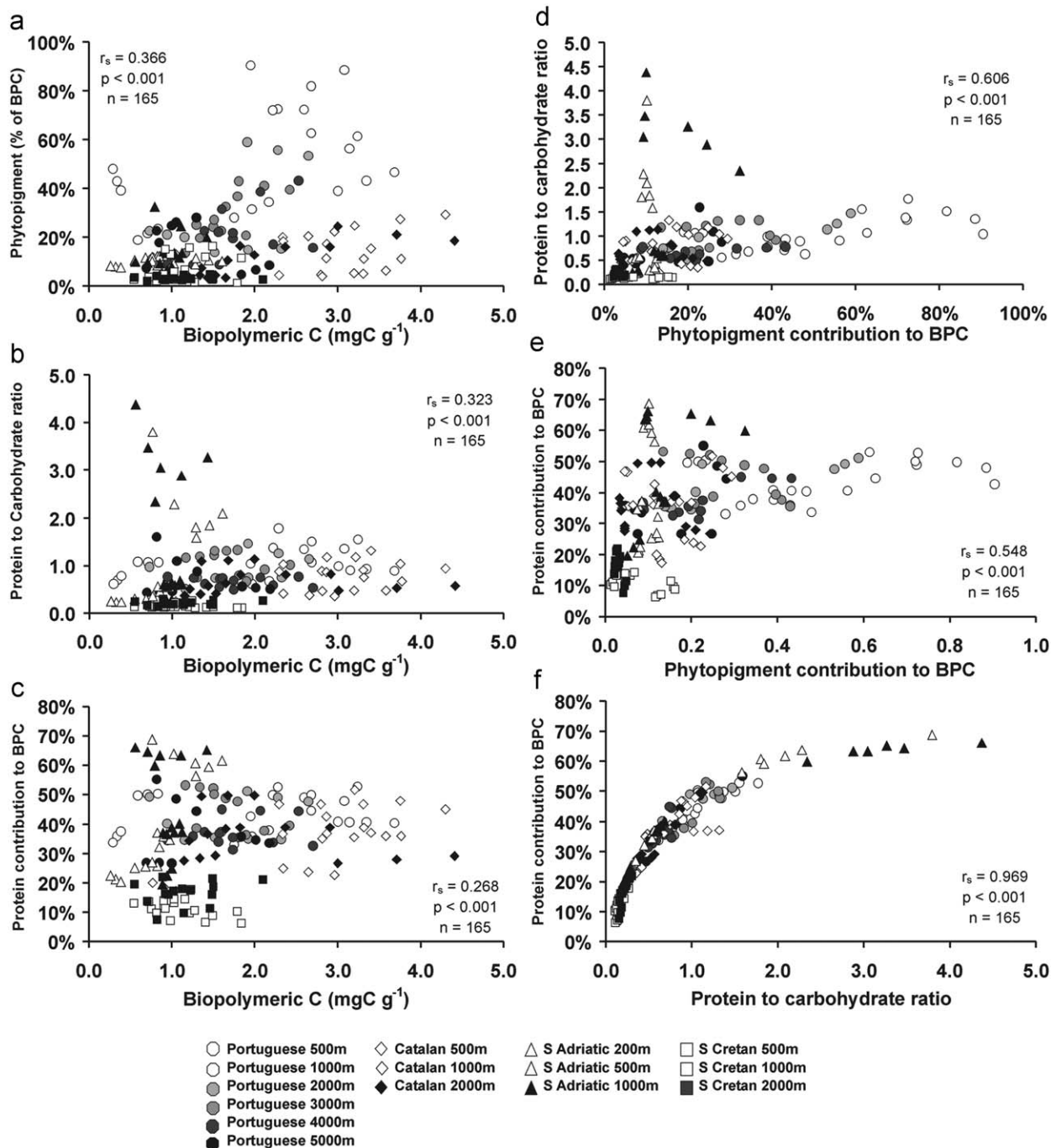
sedimentary organic matter was explained by the combination of the thermohaline conditions at the sea bottom (Table 7B), whereas within open slopes (pooled together) also the mud

fraction (expressed as percentage of the initial total dry weight) has a certain influence (Table 7C). The regression analysis carried out separately for each area showed that different sets of environmental variables were responsible for most of the variance of organic matter nutritional quality in each area (Table 8). When canyons were analysed separately, the multiple regression analysis revealed that water depth may have a significant effect on the nutritional quality of sediment organic matter in the Portuguese, Catalan and South Cretan canyons (data not shown).

#### 4. Discussion

Deep-sea environments are characterized by a lack of photosynthetic primary production in situ and, consequently, are largely dependent upon the export of organic matter from the upper photic layers (Billett et al., 1983; Smith et al., 1997; Gooday, 2002). The input of organic material to the deep typically decreases exponentially with depth, resulting in oligotrophic conditions of the deeper ocean (Smith et al., 1992; Danovaro et al., 1999a, b, 2000b; Lampitt et al., 2001). Therefore, the organic matter content and composition of deep-sea sediments is tightly linked with the overall annual production of the upper water column, the efficiency of shallow-to-deep export processes, the sedimentation rates and the preservation potential of the various molecules forming the organic matter. Normally, oceanic regions exhibit deep-sea sediment organic matter concentrations that are considerably higher than in oligotrophic oceanic regions (Tselepidis et al., 2000; Danovaro et al., 2003; Pusceddu et al., 2009a).

Our results indicate that the sediment concentrations of biochemical compounds (phytopigment, protein, carbohydrate and lipid) and biopolymeric C differ significantly between the Portuguese margin and the Mediterranean regions, consistent with previous studies that reported 3–30-fold higher concentra-



**Fig. 7.** Relationships between biopolymeric C concentrations and the protein contribution to biopolymeric C (a), the protein to carbohydrate ratio (b), the protein C contribution to biopolymeric C and the relationships between the phytopigment contribution to biopolymeric C and the protein to carbohydrate ratio (d), between the phytopigment and protein contributions to biopolymeric C (e) and the protein to carbohydrate ratio and the protein contribution to biopolymeric C (f). BPC=biopolymeric C. For all of the relationships, the Spearman rank correlation coefficient  $r_s$ , the probability level ( $p$ ) and the total number of observations ( $n$ ) are also reported.

tions of chlorophyll-*a* and 1.5–4 times higher concentration of organic carbon in the Portuguese margin than in the western Mediterranean (García et al., 2008). The consistency of these differences among sampling areas is supported either by the hypotheses-based uni- and multivariate analysis of variance, or by the visual outputs of the non-metric multidimensional scaling (Figs. 6 and 7).

We also observed significant differences in the sediment concentrations of biochemical compounds (phytopigment, protein, carbohydrate and lipid) and biopolymeric C from one

study area to the other within the Mediterranean Sea. A longitudinal gradient is evidenced irrespective of the topographic features (i.e. canyon vs. open slopes), which suggests that the productivity of the overlying water masses is the key factor controlling deep-sea benthic trophic conditions, at least for the four areas under scrutiny. We indeed report here that, overall, the mean concentrations of phytopigment and biopolymeric C in the sediments of the Portuguese and the Catalan margins are significantly higher than those in the South Adriatic and South Cretan margins (Fig. 8a–b). The same west-to-east decreasing

**Table 5**  
Results of the multivariate multiple regression analysis carried out to ascertain the role of different environmental variables on the concentrations of sediment organic matter at all sites (A), on the data from canyons (B) and open slopes (C).

|   | Explanatory variable | SS       | F      | P   | Explained variance (%) | Cumulative explained variance (%) |
|---|----------------------|----------|--------|-----|------------------------|-----------------------------------|
| A | Primary productivity | 12093.67 | 144.41 | *** | 46.98                  | 46.98                             |
|   | Bottom temperature   | 2175.50  | 31.79  | *** | 8.45                   | 55.43                             |
|   | % Mud                | 620.70   | 9.55   | *** | 2.41                   | 57.84                             |
|   | Bottom salinity      | 456.15   | 5.60   | *** | 1.77                   | 59.61                             |
|   | Water depth          | 5.98     | 0.09   | ns  | 0.02                   | 59.63                             |
|   | % Sand               | 0.01     | 0.00   | ns  | 0.00                   | 59.63                             |
| B | Primary productivity | 10795.30 | 86.06  | *** | 50.31                  | 50.31                             |
|   | Bottom temperature   | 5083.24  | 96.57  | **  | 23.69                  | 74.00                             |
|   | % Sand               | 755.61   | 6.41   | *   | 3.52                   | 77.52                             |
|   | Bottom salinity      | 506.74   | 4.47   | *   | 2.36                   | 79.88                             |
|   | Water depth          | 299.97   | 6.05   | *   | 1.40                   | 81.28                             |
|   | % Mud                | 0.03     | 0.00   | ns  | 0.00                   | 81.28                             |
| C | Primary productivity | 307.61   | 24.50  | *** | 24.38                  | 24.38                             |
|   | Bottom salinity      | 107.65   | 9.54   | **  | 8.53                   | 32.91                             |
|   | Bottom temperature   | 21.71    | 1.95   | ns  | 1.72                   | 34.63                             |
|   | Water depth          | 17.81    | 1.61   | ns  | 1.41                   | 36.04                             |
|   | % Sand               | 5.91     | 0.53   | ns  | 0.47                   | 36.51                             |
|   | % Mud                | 0.00     | 0.00   | ns  | 0.00                   | 36.51                             |

SS=sum of squares;  $F$ = $F$  statistic;  $P$ =probability level (\*\*\*= $P < 0.001$ ; \*\*= $P < 0.01$ ; ns=not significant); Chl- $a$ =chlorophyll- $a$ . The data set used for the analysis included phytopigment, protein, carbohydrate, lipid and biopolymeric C concentrations.

**Table 6**  
Results of the multivariate multiple regression analysis carried out to ascertain the role of different environmental variables on the concentrations of sediment organic matter at the investigated sites, separately for each area.

|                   | Explanatory variable | SS      | F     | P   | Explained variance (%) | Cumulative explained variance (%) |
|-------------------|----------------------|---------|-------|-----|------------------------|-----------------------------------|
| Portuguese margin | Primary productivity | 7253.96 | 49.11 | *** | 44.60                  | 44.60                             |
|                   | % Sand               | 1499.77 | 11.98 | *** | 9.22                   | 53.82                             |
|                   | Bottom temperature   | 1452.46 | 14.15 | *** | 8.93                   | 62.75                             |
|                   | Water depth          | 677.92  | 7.31  | **  | 4.17                   | 66.92                             |
|                   | Bottom salinity      | 1.47    | 0.02  | ns  | 0.01                   | 66.93                             |
|                   | % Mud                | 0.00    | 0.00  | ns  | 0.00                   | 66.93                             |
| Catalan margin    | Bottom temperature   | 625.26  | 15.49 | **  | 28.57                  | 28.57                             |
|                   | Water depth          | 316.40  | 11.50 | **  | 14.46                  | 43.03                             |
|                   | Bottom salinity      | 231.10  | 4.01  | *   | 10.56                  | 53.59                             |
|                   | % Sand               | 123.54  | 3.27  | ns  | 5.64                   | 59.23                             |
|                   | Primary productivity | 66.85   | 1.81  | ns  | 3.05                   | 62.28                             |
|                   | % Mud                | 0.00    | 0.00  | ns  | 0.00                   | 62.28                             |
| S Adriatic margin | % Sand               | 42.80   | 22.66 | *** | 42.23                  | 42.23                             |
|                   | Bottom salinity      | 20.91   | 24.54 | *** | 20.63                  | 62.86                             |
|                   | Water depth          | 9.64    | 5.91  | **  | 9.51                   | 72.37                             |
|                   | Primary productivity | 3.55    | 2.27  | ns  | 3.50                   | 75.87                             |
|                   | Bottom temperature   | 1.45    | 0.92  | ns  | 1.43                   | 77.30                             |
| S Cretan margin   | Bottom temperature   | 625.26  | 15.49 | **  | 28.57                  | 28.57                             |
|                   | Water depth          | 316.40  | 11.50 | **  | 14.46                  | 43.03                             |
|                   | Bottom salinity      | 231.10  | 4.01  | *   | 10.56                  | 53.59                             |
|                   | % Sand               | 123.54  | 3.27  | ns  | 5.64                   | 59.23                             |
|                   | Primary productivity | 66.85   | 1.81  | ns  | 3.05                   | 62.28                             |
|                   | % Mud                | 0.00    | 0.00  | ns  | 0.00                   | 62.28                             |

SS=sum of squares;  $F$ = $F$  statistic;  $P$ =probability level (\*\*\*= $P < 0.001$ ; \*\*= $P < 0.01$ ; ns=not significant); Chl- $a$ =chlorophyll- $a$ . The data set used for the analysis included phytopigment, protein, carbohydrate, lipid and biopolymeric C concentrations.

pattern is illustrated also for the nutritional quality of organic matter that, as indicated by the median values of the contribution of phytopigments to biopolymeric C and the protein to carbohydrate ratio, resulted in significantly higher values (ANOVA,  $p < 0.01$ ) in the northeastern Atlantic than in the Mediterranean Sea (Fig. 8c–d).

These results confirm previous studies on the spatial variability of sedimentary organic matter in the Mediterranean Sea, where, because of the longitudinal primary production decrease from the mesotrophic Alboran Sea to the ultra-

oligotrophic Eastern Mediterranean Sea, deep-sea sediments get progressively impoverished in organic C to the east (Danovaro et al., 1999b; Danovaro, 2003). The differences in the deep-sea benthic trophic status we report here are thus consistent with the gradient in supply of organic matter from the photic layer, as primary production and organic C fluxes in the western Mediterranean Sea are 2–4 times higher than in the eastern counterpart (Turley et al., 2000; Gambi and Danovaro, 2006) and 2–4 fold higher in the northeastern Atlantic Ocean than in the Mediterranean Sea (Morà et al., 2002).

**Table 7**

Results of the multivariate multiple regression analysis carried out to ascertain the role of different environmental variables on the values of the qualitative descriptors of sediment organic matter at all sites (A), on the data from canyons (B) and open slopes (C).

|          | Explanatory variable | SS       | F     | P   | Explained variance (%) | Cumulative explained variance (%) |
|----------|----------------------|----------|-------|-----|------------------------|-----------------------------------|
| <b>A</b> | Primary productivity | 30936.21 | 87.08 | *** | 34.82                  | 34.82                             |
|          | Bottom temperature   | 7423.60  | 26.99 | *** | 8.36                   | 43.18                             |
|          | Bottom salinity      | 6197.73  | 19.42 | *** | 6.98                   | 50.16                             |
|          | Water depth          | 1799.44  | 6.78  | *** | 2.03                   | 52.19                             |
|          | % Mud                | 210.38   | 0.79  | ns  | 0.24                   | 52.43                             |
|          | % Sand               | 0.03     | 0.00  | ns  | 0.00                   | 52.43                             |
| <b>B</b> | Primary productivity | 25484.86 | 70.24 | *** | 45.25                  | 45.25                             |
|          | Bottom temperature   | 7561.06  | 31.73 | *** | 13.42                  | 58.67                             |
|          | Bottom salinity      | 3497.25  | 10.74 | **  | 6.21                   | 64.88                             |
|          | Water depth          | 2104.77  | 9.76  | **  | 3.74                   | 68.62                             |
|          | % Mud                | 785.73   | 3.77  | *   | 1.40                   | 70.02                             |
|          | % Sand               | 0.01     | 0.00  | ns  | 0.00                   | 70.02                             |
| <b>C</b> | % Mud                | 5999.26  | 20.35 | *** | 21.12                  | 21.12                             |
|          | Bottom salinity      | 2852.41  | 10.94 | **  | 10.04                  | 31.16                             |
|          | Bottom temperature   | 2205.79  | 10.51 | **  | 7.77                   | 38.93                             |
|          | Primary productivity | 2024.03  | 8.55  | **  | 7.13                   | 46.06                             |
|          | Water depth          | 309.49   | 1.48  | ns  | 1.09                   | 47.15                             |
|          | % Sand               | 0.00     | 0.00  | ns  | 0.00                   | 47.15                             |

SS=sum of squares; F=F statistic; P=probability level (\*\*\*=P<0.001; \*\*=P<0.01; ns=not significant); Chl-a=chlorophyll-a. The data set used for the analysis included phytopigment and protein contributions to biopolymeric C and the values of the protein to carbohydrate ratio.

**Table 8**

Results of the multivariate multiple regression analysis carried out to ascertain the role of different environmental variables on the nutritional quality of sediment organic matter at the investigated sites, separately for each area.

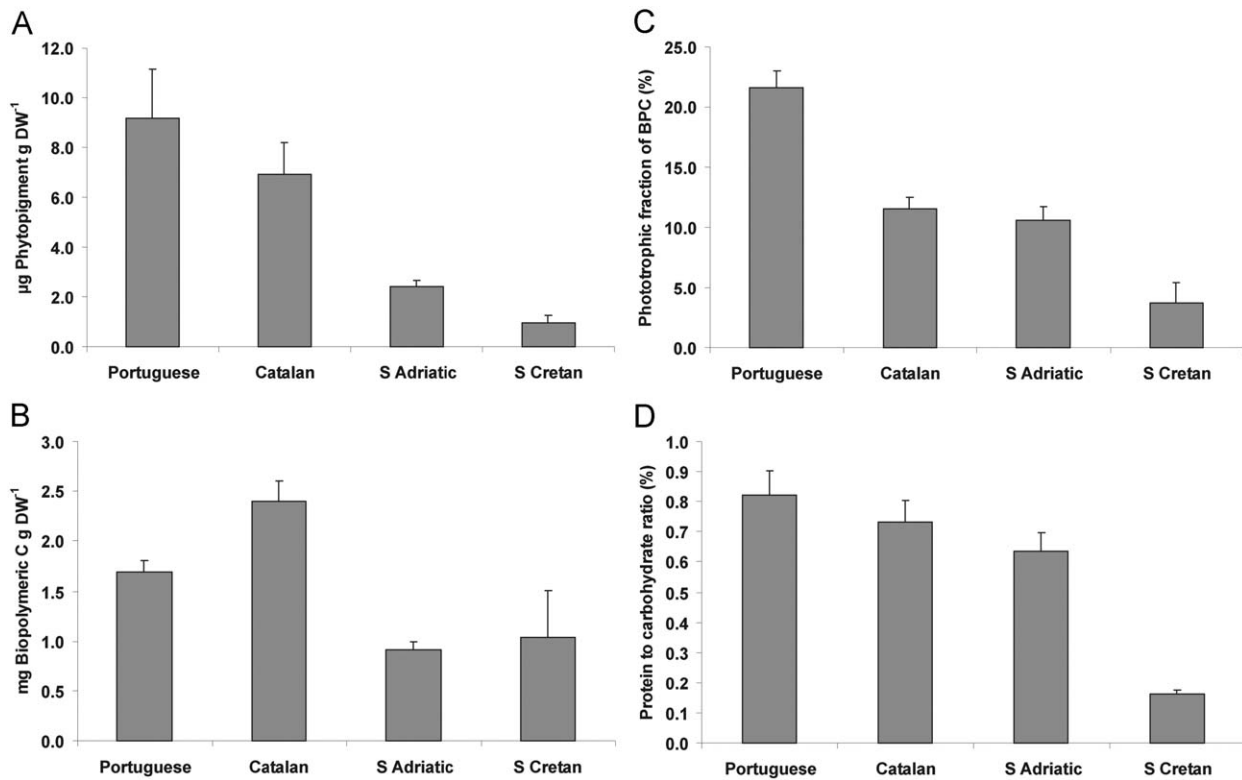
|                          | Explanatory Variable  | SS       | F       | P     | Explained variance (%) | Cumulative explained variance (%) |
|--------------------------|-----------------------|----------|---------|-------|------------------------|-----------------------------------|
| <b>Portuguese margin</b> | Primary productivity  | 10961.36 | 33.86   | ***   | 35.69                  | 35.69                             |
|                          | Bottom temperature    | 3385.10  | 12.41   | ***   | 11.02                  | 46.71                             |
|                          | % Sand                | 869.57   | 3.31    | *     | 2.83                   | 49.54                             |
|                          | Bottom salinity       | 273.87   | 1.04    | ns    | 0.89                   | 50.43                             |
|                          | Water depth           | 213.53   | 0.81    | ns    | 0.70                   | 51.13                             |
|                          | % Mud                 | 0.00     | 0.00    | ns    | 0.00                   | 51.13                             |
|                          | <b>Catalan margin</b> | % Sand   | 1872.70 | 19.00 | ***                    | 35.85                             |
| Bottom temperature       |                       | 665.08   | 8.17    | **    | 12.73                  | 48.58                             |
| Bottom salinity          |                       | 432.88   | 6.15    | *     | 8.29                   | 56.87                             |
| Primary productivity     |                       | 287.46   | 4.71    | *     | 5.50                   | 62.37                             |
| Water depth              |                       | 134.36   | 1.97    | ns    | 2.57                   | 64.94                             |
| % Mud                    |                       | 0.00     | 0.00    | ns    | 0.00                   | 64.94                             |
| <b>S Adriatic margin</b> | % Sand                | 4184.53  | 21.95   | ***   | 41.46                  | 41.46                             |
|                          | Primary productivity  | 1098.26  | 6.85    | **    | 10.88                  | 52.34                             |
|                          | Bottom temperature    | 311.23   | 2.01    | ns    | 3.08                   | 55.42                             |
|                          | Water depth           | 310.95   | 2.09    | ns    | 3.08                   | 58.50                             |
|                          | Bottom salinity       | 166.43   | 1.04    | ns    | 1.65                   | 60.15                             |
| <b>S Cretan margin</b>   | Water depth           | 480.29   | 19.51   | ***   | 38.63                  | 38.63                             |
|                          | Bottom salinity       | 115.37   | 5.34    | *     | 9.28                   | 47.91                             |
|                          | Primary productivity  | 67.44    | 3.37    | *     | 5.42                   | 53.33                             |
|                          | % Sand                | 52.55    | 2.79    | ns    | 4.23                   | 57.56                             |
|                          | Bottom temperature    | 6.91     | 0.36    | ns    | 0.56                   | 58.12                             |
|                          | % Mud                 | 0.00     | 0.00    | ns    | 0.00                   | 58.12                             |

SS=sum of squares; F=F statistic; P=probability level (\*\*\*=P<0.001; \*\*=P<0.01; ns=not significant); Chl-a=chlorophyll-a. The data set used for the analysis included the phytopigment and protein contributions to biopolymeric C and the values of the protein to carbohydrate ratio.

Recent findings shown that the basin-scale variability of organic matter quantity in the deep-sea sediments of the Mediterranean Sea is higher than the one at narrower spatial scales, i.e. from hundreds of meters to tens of kilometres (Gambi and Danovaro, 2006; Pusceddu et al., 2009b). This is again consistent with our results, as, based either on the results of uni- and multivariate analyses of variance and on the non-metric multidimensional scaling ordination, we demonstrate here that in each of our study areas the differences between physiographic features (i.e. canyons and slopes) are generally weak and,

wherever significant, such as in the Portuguese margin, are less or equally significant than the differences between areas.

The results of the multiple regression analysis carried out separately for all of the investigated areas indicate that the Portuguese margin is the only area in which the primary productivity of the upper water column layers is tightly linked with the concentrations of sediment organic matter (Table 6). As in our study, previous investigations carried out in the Portuguese margin pointed out the presence of significant differences in chlorophyll-a and organic carbon concentrations between the



**Fig. 8.** Longitudinal patterns of quantity and nutritional quality of organic matter in the deep-sea sediments of the NE Atlantic and the Mediterranean Sea. The four different panels illustrate median concentrations ( $\pm$  standard errors) calculated from all stations belonging to the same area of: (A) phytopigment, (B) biopolymeric C, (C) algal fraction of biopolymeric C and (D) protein to carbohydrate ratio.

Nazaré canyon and the adjacent open slope sediments (García and Thomsen, 2008). In this regard, Alt-Epping et al. (2007), by conducting a comprehensive investigation of the sediment organic matter origin along the Portuguese margin, highlighted the dominantly terrestrial origin of the material deposited in the Nazaré canyon, which further confirms the importance of shelf-export processes of the upper water column primary production to the deep interior of this area. Such a consistency between our and previous studies (even carried out in different seasons and using different proxies), let us hypothesise that the export of organic C from the upper water column layers to the deep Portuguese margin sediments, especially through the Nazaré canyon, is a recurrent mechanism fuelling the benthos of this area with significant amounts of organic matter characterised by high nutritional quality.

On the other hand, the lack of significant differences between canyon and open slope sediments in the Catalan and the South Cretan margins that we report here is confirmed by other previous studies even conducted in different seasons (García et al., 2008; Polymenakou et al., 2008). These findings from the Catalan, South Adriatic and South Cretan margins contrast with the evidence that deep-sea canyons and adjacent open slopes may be characterised by relevantly different modern mass fluxes and, in this sense, would question the paradigm that considers deep-sea active canyons as sole by-pass areas for the organic matter exported from the adjacent shelves. For instance, previous studies conducted in the Gulf of Lion (western Mediterranean Sea) indicate that canyon axes are more efficient in organic matter transfer to the deep than the adjacent open slopes (Buscail and Germain, 1997; Monaco et al., 1999b; Durrieu de Madron et al., 2000). Other studies suggest that canyons, with their heads at short distances from shore, easily capture sediment transported along the shelf and become active conduits for sediment funnelling from coastal

waters to the deep sea (de Stigter et al., 2007). Similarly Duineveld et al. (2001) obtained strong indications for local enrichment in organic carbon within the Whittard canyon (northeastern Atlantic) in comparison to the open slope, possibly because of enhanced transport along the canyon. Martin et al. (2006) found that total mass and organic matter downward fluxes inside the Palamós canyon (northwestern Mediterranean) are much greater than those found on the open slope, which confirms the significance of canyons in focusing across-margin transfers.

From our investigation it appears, however, that only the Nazaré and Cascais canyons in the Portuguese margin, at depths deeper than 500 m, leave a clear signal in the sediment as down-margin conveyors of high-quality organic matter. This result is in good agreement with previous studies suggesting deposition of high-quality organic matter in the Nazaré canyon jointly with present-day activity in its upper and middle reaches (de Stigter et al., 2007; García et al., 2008).

The discrepancy of the figures illustrating differences between canyons and adjacent open slopes reported in the present study may be further biased by the use of proxies with different temporal integration scales (i.e. present concentrations of organic matter in the sediment and modern mass flux patterns). In fact, processes such as sediment gravity flows and dense shelf water cascading that erode the organic-rich superficial sediment layer and redistribute the material to the lower canyon reaches and adjacent abyssal plain occur at different time scales, from seasons to decades (Durrieu de Madron et al., 2000; Heussner et al., 2006; Palanques et al., 2006; Fabres et al., 2008; Tesi et al., 2008; Sanchez-Vidal et al., 2008; Canals et al., 2009). These episodic events, which in a very short time interval can disrupt all sediment characteristics, are known also to have a strong effect on deep-sea commercially exploited species (Company et al., 2008). Other episodic events of downward sinking of water masses

altering the deep-sea trophic conditions have also been reported in the North Cretan margin and associated to severe deep-sea benthic alterations (Danovaro et al., 2004). Altogether, this evidence would suggest the need to use caution in generalising our results on longer temporal scales. However, it is worth mentioning that the Portuguese and the Catalan margins were sampled almost synoptically in autumn (late September–early October), while the South Adriatic and South Cretan margins were sampled within a short time interval in late spring (May–June). Therefore, while the differences between the westernmost areas (i.e. the Portuguese and Catalan margins) and the easternmost ones (the South Adriatic and South Cretan margins) can be explained by seasonal time lags between samplings (in autumn and spring, respectively), the differences between the Portuguese and the Catalan and those between the South Adriatic and the South Cretan margins are responsive of similar seasonal periods.

Quantity and nutritional quality of organic matter in marine sediments are often inversely related (Tselepides et al., 2000; Pusceddu et al., 2003, 2005, 2009a). In this study, this relationship was even positive (Fig. 7) and such a discrepancy, again, could be related to the fact that the data set utilised in this study did not include any appraisal of the potential temporal patterns in organic matter quantity and composition, which locally can vary greatly (Tselepides et al., 2000; Danovaro et al., 2001b; Gambi and Danovaro, 2006).

Our study indicates that, in the investigated areas, the nutritional quality and quantity of organic matter co-varied positively. Based on a meta-analysis of sedimentary data from superficial sediments worldwide, a negative relationship between biopolymeric C sediment content and the fraction of biopolymeric C associated with phytopigments has recently been observed (Pusceddu et al., 2009a). Such a negative relationship has been explained in terms of a progressive dilution of organic matter of algal origin in a more complex and heterogeneous organic matrix as the biopolymeric C content in the sediments increases. Although correlation analysis does not allow one to infer cause–effect relationships, the presence of a positive relationship between biopolymeric C sediment content and the algal fraction of biopolymeric C confirms that in the sediments under investigation, the primary productivity in the upper layers of the water column, at least at the time of sampling, was a major factor controlling either quantity and nutritional quality of sediment organic matter.

Another possible confounding of our data is likely associated with the fact that sediment deposition rates in the four investigated areas span a broad range of values, varying from  $\sim 64.5 \text{ g m}^{-2} \text{ d}^{-1}$  in the Portuguese margin (de Stigter et al., 2007), to  $4\text{--}12.5 \text{ g m}^{-2} \text{ d}^{-1}$  in the Gulf of Lions (Accornero et al., 2003),  $1.7\text{--}8.1 \text{ g m}^{-2} \text{ d}^{-1}$  in the South Adriatic margin (Turchetto et al., 2007) and  $0.2\text{--}0.5 \text{ g m}^{-2} \text{ d}^{-1}$  in the Cretan margin (Danovaro et al., 2000c). These large differences in sedimentation rates may introduce an additional problem in addressing properly the nutritional quality of sediment organic matter, as the use of a constant conversion factor of protein, carbohydrate and lipid into C equivalents would assume that all of these compounds are mineralized at the same rates. As such, the comparison between nutritional quality of sediment organic matter in so different deep-sea sediments should be considered with some caution.

Although biased by the lack of temporal replication, the overall results of the present investigation partially confirm the two null hypotheses we initially made, at least for the Mediterranean region. We indeed report here that the quantity and nutritional quality of sediment organic matter in canyons and adjacent open slopes do not show consistent depth-related patterns in all of the areas investigated. We also report that the quantity and nutritional quality of sediment organic matter in deep-sea

sediments of canyons do not differ from those in the adjacent open slopes at similar depths along the Mediterranean margins, but do differ along the Portuguese margin. We demonstrate here that differences in the benthic trophic status of deep-sea ecosystems are mostly triggered by the primary production of the upper water column layers, as expected, at least for the Mediterranean counterpart, by the well-known longitudinal gradient in productivity of the photic layers (Danovaro et al., 1999b). Part of our results contrasts with previous studies demonstrating the key trophic status peculiarities of deep-sea canyons and would therefore need further confirmation by an adequate temporal (e.g. seasonal) replication. However, this study poses a basis for more focused research on the overall landscape variability of quantity and nutritional quality of deep-sea sediment organic matter, as this is generally assumed to be a major factor controlling benthos abundance, biomass and biodiversity (Danovaro et al., 2001b).

## Acknowledgements

This study has been conducted in the framework of the Integrated Project HERMES (Hot Spot Ecosystem Research on the Margins of European Seas) funded by the European Commission under the Framework Program VI (Contract N. GOCE-CT-2005-511234-1). The authors are indebted to the crews of the ships Pelagia (The Netherlands), Universitatis and Urania (Italy), and Aegeo (Greece) for their valuable help during sea going activities. MC also acknowledges the support provided by the European SESAME (GOCE-2006-036949) and the Spanish PROMETEO (ref. CTM2007-66316-C02-01/MAR) and GRACCIE CONSOLIDER-INGENIO 2010 (CSD2007-00067) projects. GRC Geociències Marines is supported by the Generalitat de Catalunya program for excellence research groups (ref. 2005SGR00152). The authors are indebted to J.L. Casamor (GRC, Universitat de Barcelona) for the precious work in drawing Fig. 1 and A. Coluccelli (DiSMar, Polytechnic University of Marche) for elaboration of Fig. 2. The authors are also grateful to Dr. T. Trull and three anonymous reviewers for their very helpful comments and suggestions on an early version of the manuscript.

## References

- Accornero, A., Picon, P., de Bovée, F., Charrière, B., Buscail, R., 2003. Organic carbon budget at the sediment–water interface on the Gulf of Lions continental margin. *Continental Shelf Research* 23, 79–92.
- Alt-Epping, U., Mil-Homens, M., Hebbeln, D., Abrantes, F., Schneider, R.R., 2007. Provenance of organic matter and nutrient conditions on a river- and upwelling influenced shelf: a case study from the Portuguese Margin. *Marine Geology* 243, 169–179.
- Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology* 26, 32–46.
- Anderson, M.J., 2005. PERMANOVA: a FORTRAN computer program for permutational multivariate analysis of variance. Department of Statistics, University of Auckland, New Zealand.
- Anderson, M.J., ter Braak, C.J.F., 2003. Permutation tests for multi-factorial analysis of variance. *Journal of Statistical Computation and Simulation* 73, 85–113.
- Bauer, J.E., Druffel, E.R.M., 1998. Ocean margins as a significant source of organic matter to the deep open ocean. *Nature* 392, 482–485.
- Behrenfeld, M.J., Falkowski, P.G., 1997. Photosynthetic rates derived from satellite-based chlorophyll concentration. *Limnology and Oceanography* 42, 1–20.
- Bianchelli, S., Gambi, C., Pusceddu, A., Danovaro, R., 2008. Trophic conditions and meiofaunal assemblages in the Bari Canyon and the adjacent open slope (Adriatic Sea). *Chemistry and Ecology* 24 (Suppl. 1), 101–109.
- Billett, D.S.M., Lampitt, R.S., Rice, A.L., Mantoura, R.F.C., 1983. Seasonal sedimentation of phytoplankton in the deepsea benthos. *Nature* 302, 520–522.
- Bosley, K.L., Lavelle, J.W., Brodeur, R.D., Wakefield, W.W., Emmett, R.L., Baker, E.T., Rehmke, K.M., 2004. Biological and physical processes in and around Astoria submarine Canyon, Oregon, USA. *Journal of Marine Systems* 50, 21–37.
- Bousquet, P., Peylin, P., Ciais, P., Le Quéré, C., Friedlingstein, P., Tans, P.P., 2000. Regional changes in carbon dioxide fluxes of land and oceans since 1980. *Science* 290, 1342.

- Buscail, R., Germain, C., 1997. Present-day organic matter sedimentation on the NW Mediterranean margin: importance of off-shelf export. *Limnology and Oceanography* 42, 217–229.
- Canals, M., Puig, P., Durrieu de Madron, X., Heussner, S., Palanques, A., Fabres, J., 2006. Flushing submarine canyons. *Nature* 444, 354–357.
- Canals, M., Danovaro, R., Heussner, S., Lykousis, V., Puig, P., Trincardi, F., Calafat, A.M., Durrieu de Madron, X., Palanques, A., Sánchez-Vidal, A., 2009. Cascades in mediterranean submarine grand canyons. *Oceanography* 22, 26–43.
- Clarke, K.R., 1993. Non parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18, 117–143.
- Clarke, K.R., Gorley, R.N., 2001. *PRIMER v5: User manual/tutorial*, PRIMER-E, Plymouth UK, 91pp.
- Company, J.B., Puig, P., Sardà, F., Palanques, A., Latasa, M., Scharek, R., 2008. Climate influence on deep sea populations. *PLoS ONE* 3, e1431.
- Danovaro, R., 2003. Organic inputs and ecosystem efficiency in the deep Mediterranean sea. *Chemistry and Ecology* 19, 391–398.
- Danovaro, R., Fabiano, M., Della Croce, N., 1993. Labile organic matter and microbial biomasses in deep-sea sediments (Eastern Mediterranean Sea). *Deep-Sea Research I* 40, 953–965.
- Danovaro, R., Marralle, D., Della Croce, N., Parodi, P., Fabiano, M., 1999a. Biochemical composition of sedimentary organic matter and bacterial distribution in the Aegean Sea: trophic state and pelagic–benthic coupling. *Journal of Sea Research* 42, 117–129.
- Danovaro, R., Dinet, A., Duineveld, G., Tselepidis, A., 1999b. Benthic response to particulate fluxes in different trophic environments: a comparison between the Gulf of Lions–Catalan Sea (western-Mediterranean) and the Cretan Sea (eastern-Mediterranean). *Progress in Oceanography* 44, 287–312.
- Danovaro, R., Dell'Anno, A., Pusceddu, A., Marralle, D., Della Croce, N., Fabiano, M., Tselepidis, A., 2000a. Biochemical composition of pico-, nano- and micro-particulate organic matter and bacterioplankton biomass in the oligotrophic Cretan Sea (NE Mediterranean). *Progress in Oceanography* 46, 279–310.
- Danovaro, R., Tselepidis, A., Otegui, A., Della Croce, N., 2000b. Dynamics of meiofaunal assemblages on the continental shelf and deep-sea sediments of the Cretan Sea (NE Mediterranean): relationships with seasonal changes in food supply. *Progress in Oceanography* 46, 367–400.
- Danovaro, R., Della Croce, N., Dell'Anno, A., Fabiano, M., Marralle, D., Martorano, D., 2000c. Seasonal changes and biochemical composition of the labile organic matter flux in the Cretan Sea. *Progress in Oceanography* 46, 259–278.
- Danovaro, R., Dell'Anno, A., Fabiano, M., 2001a. Bioavailability of organic matter in the sediments of the Porcupine Abyssal Plain, northeastern Atlantic. *Marine Ecology Progress Series* 220, 25–32.
- Danovaro, R., Armeni, M., Dell'Anno, A., Fabiano, M., Manini, E., Marralle, D., Pusceddu, A., Vanucci, S., 2001b. Small-scale distribution of bacteria, enzymatic activities and organic matter in coastal sediments. *Microbial Ecology* 42, 177–185.
- Danovaro, R., Dell Croce, N., Dell'Anno, A., Pusceddu, A., 2003. A depocenter of organic matter at 7800 m depth in the SE Pacific Ocean. *Deep-Sea Research I* 50, 1411–1420.
- Danovaro, R., Della'Anno, A., Pusceddu, A., 2004. Biodiversity response to climate change in a warm deep sea. *Ecology Letters* 7, 821–828.
- de Stigter, H., Boer, W., de Jesus Mendes, P.A., Jesus, C.C., Thomsen, L., van den Bergh, G., van Weering, S.E., 2007. Recent sediment transport and deposition in the Nazaré Canyon, Portuguese continental margin. *Marine Geology* 246, 144–164.
- Dell'Anno, A., Danovaro, R., 2005. Extracellular DNA plays a key role in deep-sea ecosystem functioning. *Science* 309, 2179.
- Dell'Anno, A., Mei, M.L., Pusceddu, A., Danovaro, R., 2002. Assessing the trophic state and eutrophication of coastal marine systems: a new approach based on the biochemical composition of sediment organic matter. *Marine Pollution Bulletin* 44, 611–622.
- Dell'Anno, A., Incera, M., Mei, M.L., Pusceddu, A., 2003. Mesoscale variability of organic matter composition in NW Adriatic sediments. *Chemistry and Ecology* 19, 33–45.
- Dickens, G.R., 2003. Rethinking the global carbon cycle with a large, dynamic and microbially mediated gas hydrate capacitor. *Earth and Planetary Science Letters* 213, 169–183.
- Duineveld, G., Lavaleye, M., Berghuis, E., de Wilde, P., 2001. Activity and composition of the benthic fauna in the Whittard Canyon and the adjacent continental slope (NE Atlantic). *Oceanologica Acta* 24, 69–83.
- Durrieu de Madron, X., 1994. Hydrography and nepheloid structures in the Grand-Rhone canyon. *Continental Shelf Research* 14, 457–477.
- Durrieu de Madron, X., Radakovitch, O., Heussner, S., Loye-Pilot, M.D., Monaco, A., 1999. Role of the climatological and current variability on shelf-slope exchanges of particulate matter: evidence from the Rhone continental margin (NW Mediterranean). *Deep-Sea Research I* 46, 1513–1538.
- Durrieu de Madron, X., Abassi, A., Heussner, S., Monaco, A., Aloisi, J.C., Radakovitch, O., Giresse, P., Buscail, R., Kerhervé, P., 2000. Particulate matter and organic carbon budgets for the Gulf of Lions (NW Mediterranean). *Oceanologica Acta* 23, 717–730.
- Epping, E., van der Zee, C., Soetaert, K., Helder, W., 2002. On the oxidation and burial of organic carbon in sediments of the Iberian margin and Nazaré Canyon (NE Atlantic). *Progress in Oceanography* 52, 399–431.
- Etcheber, H., Relexans, J.C., Beliard, M., Weber, O., Buscail, R., Heussner, S., 1999. Distribution and quality of sedimentary organic matter on the Aquitanian margin (Bay of Biscay). *Deep-Sea Research II* 46, 2249–2288.
- Fabiano, M., Danovaro, R., Fraschetti, S., 1995. A three-year time series of elemental and biochemical composition of organic matter in subtidal sandy sediments of the Ligurian Sea (north western Mediterranean). *Continental Shelf Research* 15, 1453–1469.
- Fabiano, M., Pusceddu, A., Dell'Anno, A., Armeni, M., Vanucci, S., Lampitt, R.S., Wolff, G.A., Danovaro, R., 2001. Fluxes of phytopigments and labile organic matter to the deep ocean in the NE Atlantic Ocean. *Progress in Oceanography* 50, 89–104.
- Fabres, J., Tesi, T., Velez, J., Batista, F., Lee, C., Calafat, A., Heussner, S., Palanques, A., Miserocchi, S., 2008. Seasonal and event-controlled export of organic matter from the shelf towards the Gulf of Lions continental slope. *Continental Shelf Research* 28, 1971–1983.
- Flexas, M.M., Durrieu de Madron, X., García, M.A., Canals, M., Arnau, P., 2002. Flow variability in the Gulf of Lions during the MATER HFF experiment (March–May 1997). *Journal of Marine Systems* 33–34, 197–214.
- Gambi, C., Danovaro, R., 2006. A multiple-scale analysis of metazoan meiofaunal distribution in the deep Mediterranean Sea. *Deep-Sea Research I* 53, 1117–1134.
- García, R., Thomsen, L., 2008. Bioavailable organic matter in surface sediments of the Nazaré canyon and adjacent slope (Western Iberian Margin). *Journal of Marine Systems* 74, 44–59.
- García, R., van Oevelen, D., Soetaert, K., Thomsen, L., De Stigter, H.C., Epping, E., 2008. Deposition rates, mixing intensity and organic content in two contrasting submarine canyons. *Progress in Oceanography* 76, 192–215.
- Gooday, A.J., 2002. Biological responses to seasonally varying fluxes of organic matter to the ocean floor: a review. *Journal of Oceanography* 58, 305–332.
- Heussner, S., Durrieu de Madron, X., Calafat, A., Canals, M., Carbonne, J., Delsaut, N., Saragoni, G., 2006. 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). *Marine Geology* 234, 63–92.
- Lampitt, R.S., Bett, B.J., Kiriakoulakis, K., Popova, E.E., Ragueneau, O., Vangriesheim, A., Wolff, G.A., 2001. Material supply to the abyssal seafloor in the northeast Atlantic. *Progress in Oceanography* 50, 27–63.
- Lastras, G., Arzola, R.G., Masson, D.G., Wynn, R.B., Huvenne, V.A.I., Hühnerbach, V., Canals, M., 2009. Geomorphology and sedimentary features in the Central Portuguese submarine canyons, Western Iberian margin. *Geomorphology* 103, 310–329.
- Lewis, K.B., Barnes, P.M., 1999. Kaikoura Canyon, New Zealand: active conduit from near-shore sediment zones to trench-axis channel. *Marine Geology* 162, 39–69.
- Lorenzen, C., Jeffrey, J., 1980. Determination of chlorophyll in seawater. *Technical Paper in Marine Science (UNESCO)* 35, 1–20.
- Martin, J., Palanques, A., Puig, P., 2006. Composition and variability of downward particulate matter fluxes in the Palamós submarine canyon (NW Mediterranean). *Journal of Marine Systems* 60, 75–97.
- McArdle, B.H., Anderson, M.J., 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology* 82, 290–297.
- Monaco, A., Biscaye, P.E., Laborde, P., 1999a. The ECOFER (ÉCOsystème du canyon du cap-FERret) experiment in the Bay of Biscay: introduction, objectives and major results. *Deep-Sea Research II* 46, 1967–1978.
- Monaco, A., Durrieu de Madron, X., Radakovitch, O., Heussner, S., Carbonne, J., 1999b. Origin and variability of downward biogeochemical fluxes on the Rhone continental margin (NW Mediterranean). *Deep-Sea Research I* 46, 1483–1511.
- Moran, X.A.G., Estrada, M., Gasol, J.M., Pedrós-Alió, C., 2002. Dissolved primary production and the strength of phytoplankton–bacterioplankton coupling in contrasting marine regions. *Microbial Ecology* 44, 217–223.
- Mullenbach, B.L., Nittrouer, C.A., 2000. Rapid deposition of fluvial sediment in the Eel Canyon, northern California. *Continental Shelf Research* 20, 2191–2212.
- Palanques, A., García-Ladona, E., Gomis, D., Martín, J., Marcos, M., Pascual, A., Puig, P., Gili, J.M., Emelianov, M., Monserrat, S., Guillén, J., Tintoré, J., Segura, M., Jordi, A., Ruiz, S., Basterretxea, G., Font, J., Blasco, D., Pagès, F., 2005. General patterns of circulation, sediment fluxes and ecology of the Palamós (La Fonera) submarine canyon, northwestern Mediterranean. *Progress in Oceanography* 66, 89–119.
- Palanques, A., Durrieu de Madron, X., Puig, P., Fabres, J., Guillén, J., Calafat, A., Canals, M., Heussner, S., Bonnín, J., 2006. Suspended sediment fluxes and transport processes in the Gulf of Lions submarine canyons. The role of storms and dense water cascading. *Marine Geology* 234, 43–61.
- Pinckney, J., Papa, R., Zingmark, R., 1994. Comparison of high-performance liquid chromatographic, spectrophotometric, and fluorometric methods for determining chlorophyll *a* concentrations in estuarine sediments. *Journal of Microbiological Methods* 19, 59–66.
- Polymenakou, P.N., Lampadariou, N., Tselepidis, A., 2008. Exo-enzymatic activities and organic matter properties in deep-sea canyon and slope systems off the southern Cretan margin. *Deep-Sea Research I* 55, 1318–1329.
- Puig, P., Palanques, A., Guille, J., García-Ladona, E., 2000. Deep slope currents and suspended particle fluxes in and around the Foix submarine canyon (NW Mediterranean). *Deep-Sea Research I* 47, 343–366.
- Puig, P., Ogston, A.S., Mullenbach, B.L., Nittrouer, C.A., Sternberg, R.W., 2003. Shelf-to-canyon sediment-transport processes on the Eel continental margin (northern California). *Marine Geology* 193, 129–149.
- Pusceddu, A., Sarà, G., Armeni, M., Fabiano, M., Mazzola, A., 1999. Seasonal and spatial changes in the sediment organic matter of a semi-enclosed marine system (W-Mediterranean Sea). *Hydrobiologia* 397, 59–70.



- Pusceddu, A., Dell'Anno, A., Fabiano, M., 2000. Organic matter composition in coastal sediments at Terra Nova Bay (Ross Sea) during summer 1995. *Polar Biology* 23, 288–293.
- Pusceddu, A., Dell'Anno, A., Manini, E., Fabiano, M., Sarà, G., Danovaro, R., 2003. 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.
- Pusceddu, A., Dell'Anno, A., Fabiano, M., Danovaro, R., 2004. Quantity and biochemical composition of organic matter in marine sediments. *Biologia Marina Mediterranea* 11, 39–53.
- Pusceddu, A., Fiordelmondo, C., Polymenakou, P., Polychronaki, T., Tselepides, A., Danovaro, R., 2005. Effects of bottom trawling on the quantity and biochemical composition of organic matter in coastal marine sediments (Thermaikos Gulf, northwestern Aegean Sea). *Continental Shelf Research* 25, 2491–2505.
- Pusceddu, A., Dell'Anno, A., Fabiano, M., Danovaro, R., 2009a. Quantity and bioavailability of sediment organic matter as signatures of benthic trophic status. *Marine Ecology Progress Series* 375, 41–52.
- Pusceddu, A., Gambi, C., Zeppilli, D., Bianchelli, S., Danovaro, R., 2009b. Organic matter composition, metazoan meiofauna, and nematode biodiversity in sediments of the deep Mediterranean Sea. *Deep-Sea Research II* 56, 755–762.
- Rogers, A., Billett, D., Berger, W., Flach, E., Freiwald, A., Gage, J., Hebbeln, D., Heip, C., Pfannkuche, O., Ramirez-Llodra, E., Medlin, L., Sibuet, M., Soetaert, K., Tendal, O., Vanreusel, A., Włodarska-Kowalczyk, M., 2003. Life at the edge: achieving prediction from environmental variability and biological variety. In: Wefer, G., Billett, D.S.M., Hebbeln, D., Jørgensen, B.B., Schlüter, M., van Weering, T.C.E. (Eds.), *Ocean Margin Systems*. Springer-Verlag, Berlin, pp. 387–404.
- Sanchez-Vidal, A., Pasqual, C., Kerhervé, P., Calafat, A., Heussner, S., Palanques, A., Durrieu de Madron, X., Canals, M., Puig, P., 2008. Impact of dense shelf water cascading on the transfer of organic matter to the deep western Mediterranean basin. *Geophysical Research Letters* 35, 1–5.
- Schmidt, S., de Stigter, H.C., van Weering, T.C.E., 2001. Enhanced short-term sediment deposition within the Nazaré Canyon, North-East Atlantic. *Marine Geology* 173, 55–67.
- Searle, S.R., Cassella, G., McCulloch, C.E., 1992. *Variance Components*. Wiley, New York.
- Skliris, N., Djenidi, S., 2006. Plankton dynamics controlled by hydrodynamic processes near a submarine canyon off NW Corsican coast: a numerical modelling study. *Continental Shelf Research* 26, 1336–1358.
- Smith Jr., K.L., Baldwin, R.J., Williams, P.M., 1992. Reconciling particulate organic carbon flux and sediment community oxygen consumption in the deep North Pacific. *Nature* 359, 131–136.
- Smith, C.R., Berelson, W., Demaster, D.J., Dobbs, F.C., Hammound, D., Hoover, D.J., Pope, R.H., Stephens, M., 1997. Latitudinal variations in benthic processes in the abyssal equatorial Pacific: control by biogenic particle flux. *Deep-Sea Research II* 44, 2295–2317.
- Szymczak-Żyła, M., Kowalewska, G., 2007. Chloropigments *a* in the Gulf of Gdańsk (Baltic Sea) as markers of the state of this environment. *Marine Pollution Bulletin* 55, 512–528.
- Tesi, T., Langone, L., Goñi, M.A., Turchetto, M., Miserocchi, S., Boldrin, A., 2008. Source and composition of organic matter in the Bari canyon (Italy): Dense water cascading versus particulate export from the upper ocean. *Deep-Sea Research I* 55, 813–831.
- Tselepides, A., Polychronaki, T., Marrale, D., Akoumianaki, I., Dell'Anno, A., Pusceddu, A., Danovaro, R., 2000. Organic matter composition of the continental shelf and bathyal sediments of the Cretan Sea (NE Mediterranean). *Progress in Oceanography* 46, 311–344.
- Turchetto, M., Boldrin, A., Langone, L., Miserocchi, S., Tesi, T., Fogliani, F., 2007. Particle transport in the Bari Canyon (southern Adriatic Sea). *Marine Geology* 246, 231–247.
- Turley, C.M., Bianchi, M., Christaki, U., Conan, P., Harris, J.R.W., Psarra, S., Ruddy, G., Stutt, E.D., Tselepides, A., Van Wambeke, F., 2000. Relationship between primary producers and bacteria in an oligotrophic sea—the Mediterranean and biochemical implications. *Marine Ecology Progress Series* 193, 11–18.
- Underwood, A.J., 1991. Beyond BACI: experimental designs for detecting human environmental impacts on temporal variations in natural populations. *Australian Journal of Marine Freshwater Research* 42, 569–587.
- Walsh, J.J., 1991. Importance of continental margins in the marine biogeochemical cycling of carbon and nitrogen. *Nature* 350, 53–55.
- Weaver, P.E., Billett, D.M., Boetius, A., Danovaro, R., Freiwald, A., Sibuet, M., 2004. Hotspot ecosystem research on Europe's deep-ocean margins. *Oceanography* 17, 132–143.