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

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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.

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).

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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

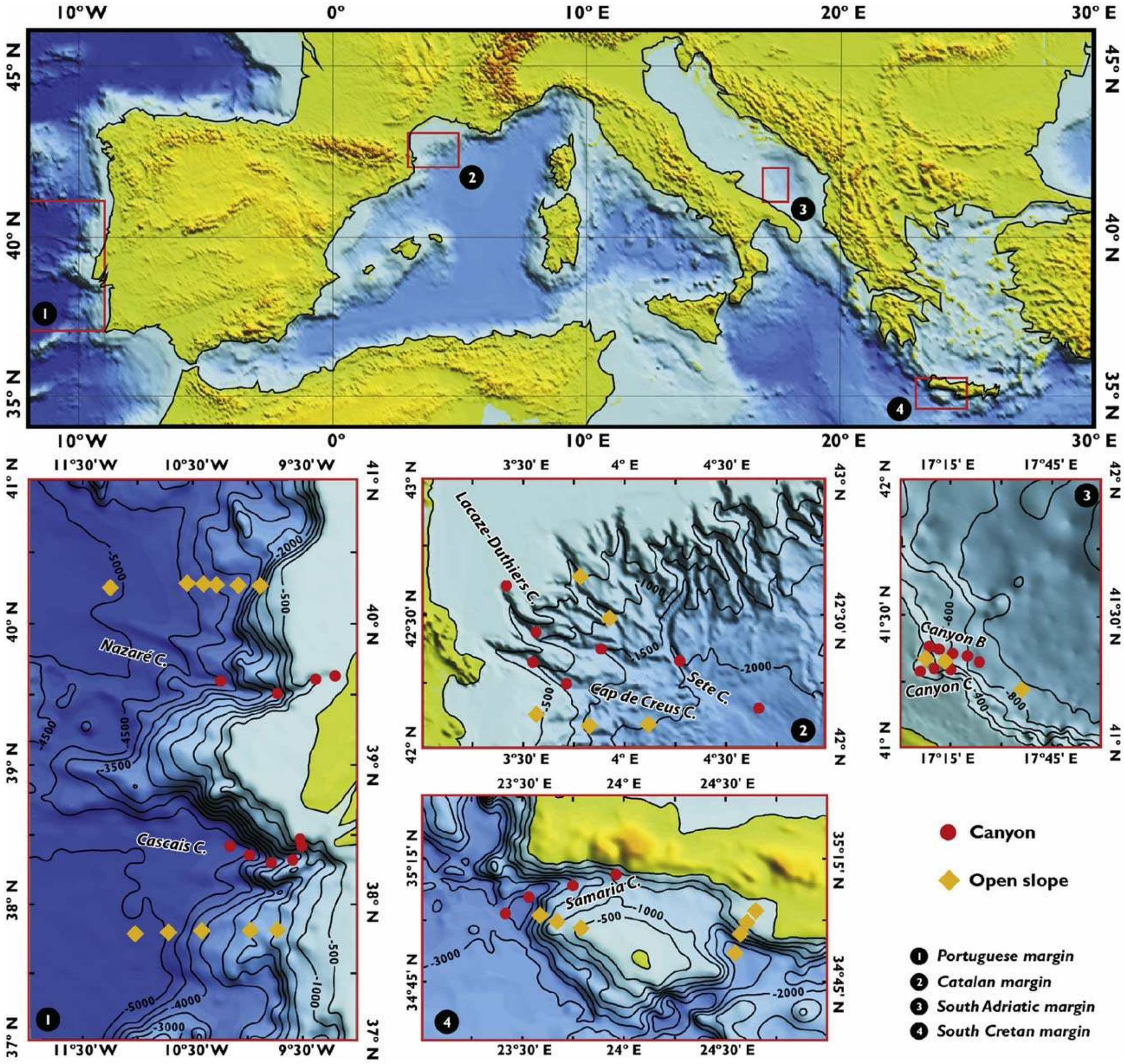

Fig. 1. Sampling area and station locations.

and the open slopes did not show particular patterns (Lykoussis 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-μm sieve and the two fractions (sands $>63\,\mu m$, and mud $<63\,\mu m$) weighed (± 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 μl 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).

Table 1
Location, depth, grain size, bottom temperature and salinity and concentrations of organic compounds (± sd=standard deviation) in the sediments of the investigated areas.

Margin	Setting	Station	Latitude (N)	Longitude (E)	Depth (m)	Grain size		*T* (°C)	Salinity	Phytopigments		Proteins		Carbohydrates		Lipids		Biopolymeric C	
						Silt (%)	Mud (%)			µg g^{-1}	sd	mg g^{-1}	sd	mg g^{-1}	sd	mg g^{-1}	sd	mg C g^{-1}	sd
Portuguese	**N open slope**	64PE952-8	40°10.00′	−09°40.03′	416	63	37	11.35	35.55	3.67	0.14	0.25	0.05	0.36	0.03	0.10	0.02	0.34	0.05
		64PE952-7	40°10.00′	−09°50.00′	959	43	57	10.69	36.09	3.84	1.05	0.72	0.13	0.68	0.12	0.11	0.01	0.71	0.12
		64PE952-6	40°10.01′	−09°56.00′	1463	51	49	8.59	35.88	4.94	0.83	0.77	0.04	1.17	0.42	0.13	0.03	0.94	0.21
		64PE952-4	40°10.00′	−09°59.99′	3475	42	58	2.57	34.84	6.54	2.61	1.43	0.17	1.20	0.12	0.20	0.05	1.33	0.17
		64PE952-3	40°09.99′	−10°10.01′	3981	27	73	2.52	34.82	9.50	1.08	1.53	0.26	2.60	0.74	0.58	0.07	2.22	0.48
		64PE952-1	40°10.01′	−10°59.99′	4902	27	73	2.47	34.86	3.41	1.23	1.41	0.07	2.67	0.25	0.33	0.05	2.01	0.17
	Nazaré canyon	64PE952-44	39°36.81′	−09°11.42′	485	59	41	12.15	35.81	46.90	2.90	2.59	0.90	1.94	0.31	0.73	0.11	2.59	0.65
		64PE952-43	39°35.80′	−09°24.23′	897	42	58	11.64	36.09	42.09	2.21	2.43	0.18	2.28	0.63	0.77	0.17	2.68	0.47
		64PE952-40	39°30.24′	−09°50.60′	3231	16	84	2.63	34.87	21.70	2.29	1.63	0.32	1.78	0.14	0.81	0.13	2.12	0.31
		64PE952-49	39°35.60′	−10°20.00′	4363	28	72	2.49	34.80	20.02	7.36	1.88	0.41	2.49	0.51	0.20	0.08	2.07	0.46
	Cascais canyon	64PE952-35	38°29.61′	−09°28.73′	445	48	52	11.85	35.74	36.21	6.93	2.77	0.27	2.99	0.44	1.06	0.05	3.35	0.34
		64PE952-36	38°27.91′	−09°28.49′	1021	54	46	12.05	36.28	54.81	13.42	2.73	0.28	1.81	0.42	0.83	0.13	2.68	0.40
		64PE952-32	38°21.79′	−09°30.58′	2100	61	39	4.77	35.20	31.76	3.61	2.28	0.29	1.82	0.46	0.58	0.06	2.28	0.37
		64PE952-31	38°18.69′	−09°42.15′	2975	61	39	2.85	34.95	13.37	3.14	1.64	0.10	1.25	0.07	0.46	0.09	1.65	0.14
		64PE952-30	38°20.00′	−09°51.51′	3914	76	24	2.48	34.91	8.68	0.77	1.08	0.02	1.99	0.26	0.32	0.08	1.56	0.17
		64PE952-60	38°25.01′	−10°05.00′	4689	45	55	2.51	34.90	3.76	2.45	0.46	0.08	1.02	0.15	0.28	0.07	0.85	0.15
	S open slope	64PE952-56	37°49.97′	−9°30.88′	1002	78	22	11.60	36.29	15.45	3.19	1.43	0.25	2.32	0.16	0.44	0.03	1.96	0.21
		64PE952-54	37°50.00′	−9°45.00′	2130	36	64	5.45	35.34	7.14	1.85	1.37	0.27	1.84	0.35	0.68	0.17	1.92	0.40
		64PE952-52	37°50.00′	−10°05.00′	2908	31	69	2.75	34.95	9.00	0.88	1.22	0.19	1.72	0.36	0.42	0.08	1.60	0.30
		64PE952-51	37°50.01′	−10°30.01′	3908	47	53	2.43	34.88	2.80	0.63	0.92	0.26	1.25	0.38	0.41	0.05	1.26	0.31
		64PE952-50	37°50.01′	−11°00.01′	4987	60	40	2.55	34.90	6.88	2.24	1.04	0.13	0.96	0.39	0.21	0.03	1.06	0.24
Catalan	**N open slope**	NOS 450	42°34.13′	3°39.19′	334	29	71	13.51	38.30	3.45	0.85	2.67	0.48	2.99	0.48	0.40	0.10	2.80	0.51
		NOS 1000	42°26.49′	3°51.32′	1022	23	77	13.18	38.47	4.31	1.51	2.32	0.31	4.89	0.54	0.14	0.03	3.20	0.39
	Lacaze-duthiers canyon	CLD 450	42°34.44′	3°24.04′	434	24	76	13.33	38.52	25.75	5.87	3.67	0.29	3.53	0.65	0.73	0.19	3.76	0.55
		CLD 1000	42°26.56′	3°31.83′	990	20	80	13.25	38.51	9.39	1.18	2.63	0.14	3.51	0.60	0.83	0.19	3.32	0.45
		CLD 1500	42°21.96′	3°49.41′	1497	44	56	12.99	38.44	4.48	1.91	1.69	0.32	1.52	0.26	0.32	0.07	1.68	0.32
	Cap de creus canyon	CCC 450	42°18.47′	3°36.60′	960	20	80	13.01	38.45	13.64	2.87	1.28	0.09	3.37	0.51	0.90	0.08	2.65	0.31
		CCC 1000	42°12.64′	3°49.22′	1434	14	86	13.02	38.44	19.53	1.18	2.12	0.49	3.97	0.61	1.44	0.30	3.71	0.70
		CLD 2000	42°12.88′	4°15.43′	1874	32	68	13.04	38.44	1.28	0.12	1.07	0.22	1.86	0.17	0.22	0.05	1.43	0.22
	Sete canyon	CS 2400	42°04.78′	4°40.90′	2342	29	71	13.10	38.43	9.54	2.06	1.88	0.43	2.31	0.50	0.70	0.17	2.37	0.54
	S open slope	SOS 450	42°08.85′	3°35.06′	398	31	69	13.34	38.49	12.40	0.67	2.16	0.41	1.83	0.12	1.44	0.37	2.87	0.53
		SOS 1000	42°07.72′	3°46.63′	985	13	87	13.02	38.45	2.86	0.56	0.34	0.03	1.33	0.19	0.28	0.06	0.91	0.14
		SOS 1900	42°07.05′	4°02.74′	1887	23	77	13.07	38.44	1.51	0.20	0.78	0.13	1.98	0.22	0.22	0.05	1.34	0.19
S Adriatic	**Canyon B**	SE06-26	41°22.10′	17°06.70′	370	61	39	13.22	38.66	2.60	0.31	0.56	0.14	1.24	0.04	0.11	0.00	0.85	0.09
		SE06-12	41°21.71′	17°07.75′	446	35	65	13.22	38.66	1.77	0.03	0.65	0.03	1.19	0.08	0.14	0.04	0.90	0.07
		SE06-3	41°20.63′	17°11.02′	590	81	19	13.23	38.65	1.56	0.43	0.43	0.07	1.73	0.03	0.05	0.01	0.94	0.05
	Open slope	SE06-24	41°21.30′	17°05.96′	196	89	11	13.22	38.66	2.01	0.54	0.36	0.07	1.18	0.23	0.05	0.01	0.68	0.14
		SE06-2	41°20.08′	17°10.32′	406	56	44	13.22	38.66	2.40	0.45	1.33	0.26	0.58	0.30	0.18	0.01	1.02	0.26
		SE06-37	41°13.70′	17°35.15′	908	32	68	12.96	38.63	6.80	0.33	1.44	0.46	0.50	0.08	0.28	0.07	1.11	0.31
	Canyon C	SE06-18	41°19.07′	17°05.15′	341	99	1	12.97	38.65	0.63	0.10	0.14	0.02	0.59	0.12	0.02	0.01	0.32	0.06
		SE06-8	41°19.47′	17°09.75′	435	37	63	13.10	38.65	3.90	0.18	1.75	0.27	0.95	0.02	0.28	0.03	1.45	0.16
		SE06-7	41°18.18′	17°12.51′	593	43	57	12.86	38.64	3.20	0.04	0.79	0.11	1.22	0.10	0.16	0.01	1.00	0.10
		SE06-28	41°18.84′	17°14.66′	618	52	48	12.85	38.64	1.71	0.31	0.93	0.18	0.27	0.10	0.19	0.03	0.71	0.15
		SE06-27	41°18.43′	17°15.61′	721	42	58	12.74	38.63	3.52	0.32	0.78	0.07	1.31	0.10	0.17	0.02	1.03	0.09
S Cretan	**Samaria canyon**	HCM3MC88	35°11.58′	23°56.04′	1216	37	63	13.60	38.76	0.69	0.29	0.20	0.04	1.38	0.21	0.10	0.01	0.72	0.18
		HCM3MC94	35°08.85′	23°42.85′	2420	11	89	13.50	38.76	0.53	0.11	0.30	0.08	1.58	0.22	0.18	0.01	0.92	0.21
		HCM3MC47	35°05.08′	23°33.22′	3553	65	35	13.60	38.75	0.97	0.19	0.44	0.10	2.04	0.27	0.27	0.04	1.23	0.27
		HCM3MC78	35°03.15′	23°29.53′	3600	4	96	13.60	38.75	1.00	0.21	0.65	0.15	2.34	0.69	0.32	0.03	1.49	0.60
	***W* open slope**	HCM3MC90	34°59.01′	23°48.57′	520	54	46	13.90	38.85	1.50	0.39	0.28	0.05	1.98	0.13	0.14	0.01	1.03	0.13
		HCM3MC89	35°00.68′	23°41.83′	1081	23	77	13.70	38.75	0.50	0.05	0.27	0.05	2.48	0.64	0.19	0.02	1.27	0.52
		HCM3MC86	35°01.69′	23°36.86′	1903	15	85	13.70	38.70	0.79	0.13	0.36	0.06	1.82	0.57	0.16	0.01	1.02	0.47
	***E* open slope**	HCM3MC80	34°59.88′	24°38.84′	216	20	80	15.00	38.94	4.28	0.81	0.19	0.04	1.61	0.45	0.90	0.20	1.41	0.43
		HCM3MC81	34°59.03′	24°37.14′	590	2	98	13.80	38.80	4.78	1.15	0.24	0.02	1.75	0.26	0.52	0.19	1.21	0.29
		HCM3MC82	34°57.16′	24°35.49′	1176	3	97	13.60	38.76	0.69	0.21	0.30	0.13	1.42	0.19	0.42	0.01	1.03	0.21
		HCM3MC83	34°52.99′	24°32.87′	2669	4	96	13.60	38.74	1.32	0.30	0.23	0.08	1.33	0.36	0.67	0.02	1.15	0.32

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 $\mu g\,C\,g^{-1}$.

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 $mgC\,mg^{-1}$, 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; Tselepides 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 matrixes 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

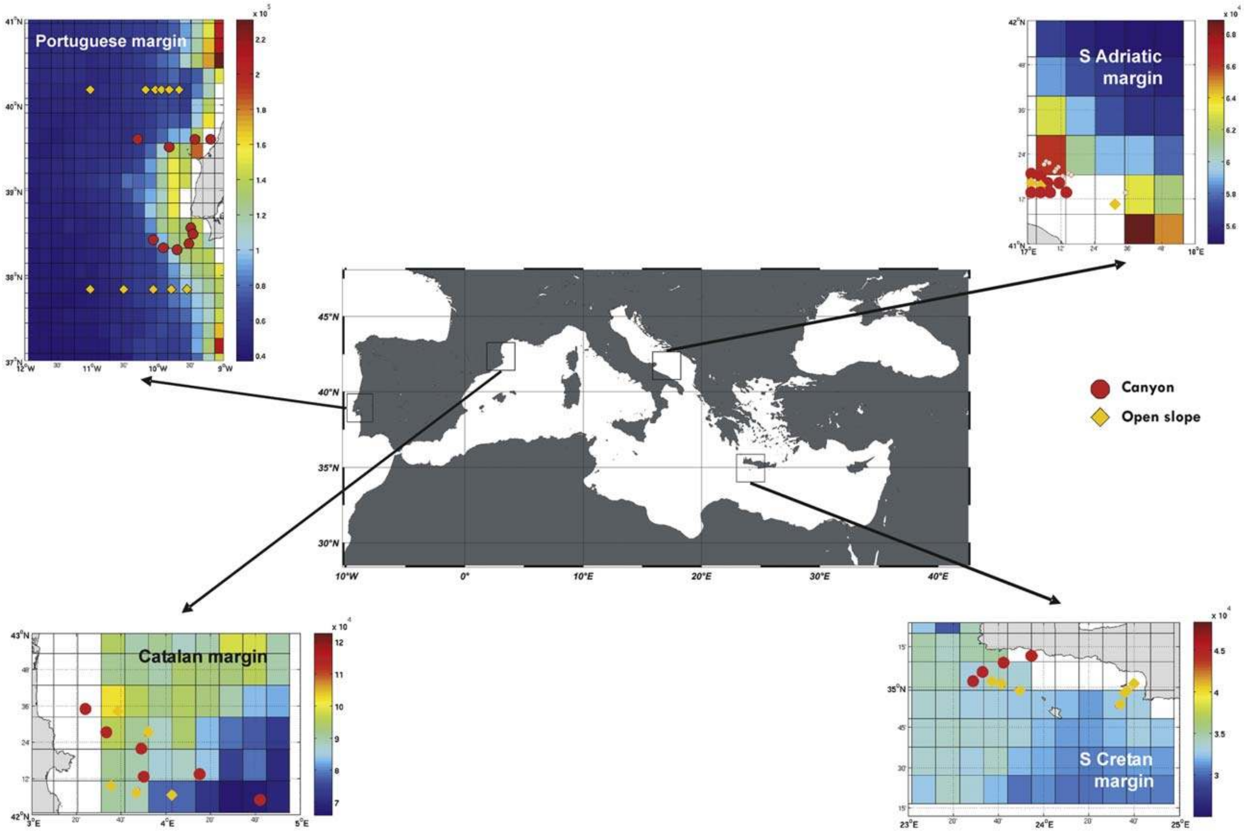

Fig. 2. Primary productivity spatial patterns in the four study areas.

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 ± 0.05 in the western Cretan slope at 1081 m depth to $55 \pm 13\,\mu g\,g^{-1}$ in the Cascais canyon at 1021 m water depth. The protein concentrations ranged from 0.14 ± 0.02 in canyon C at 341 m depth to $3.67 \pm 0.29\,mg\,g^{-1}$ in the Lacaze-Duthiers canyon at 434 m depth. The carbohydrate concentrations ranged from 0.36 ± 0.03 in the northern Portuguese open slope at 416 m depth to $4.\ 9 \pm 0.5\,mg\,g^{-1}$ in the northern Catalan open slope at 1022 m depth. The lipid concentrations ranged from 0.02 ± 0.01 to $1.4 \pm 0.4\,mg\,g^{-1}$, 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 ± 0.06 to $3.8 \pm 0.6\,mg\,g^{-1}$ 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).

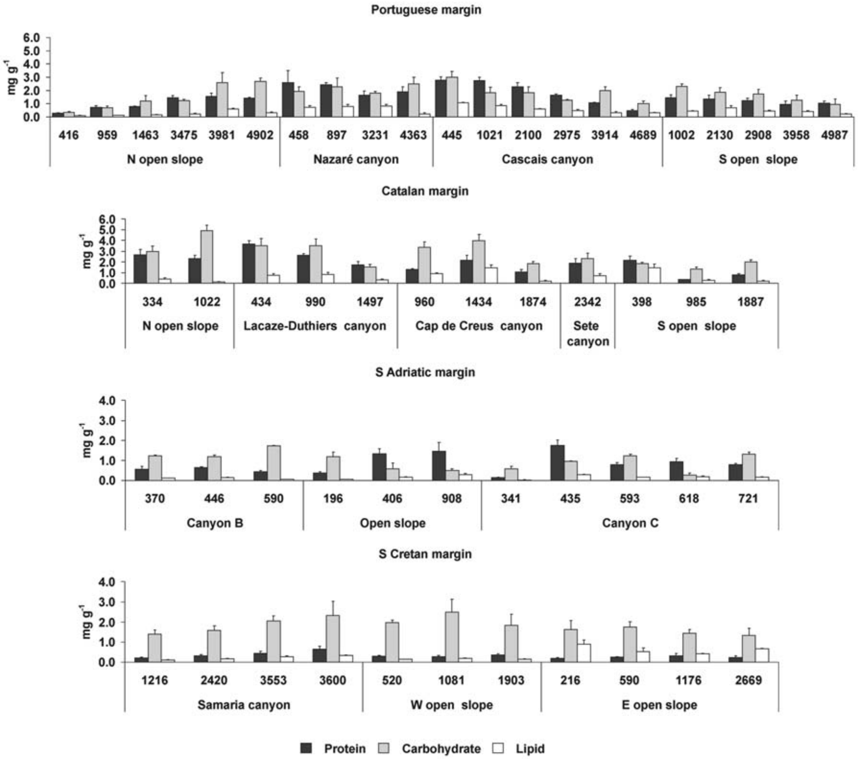

Fig. 3. Protein, carbohydrate and lipid contents in the sediment of all of the 55 stations along the Portuguese, Catalan, South Adriatic and South Cretan margins. Illustrated are values (± standard deviation of $n=3$ replicates) from the four investigated areas, divided by open slope and canyon settings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

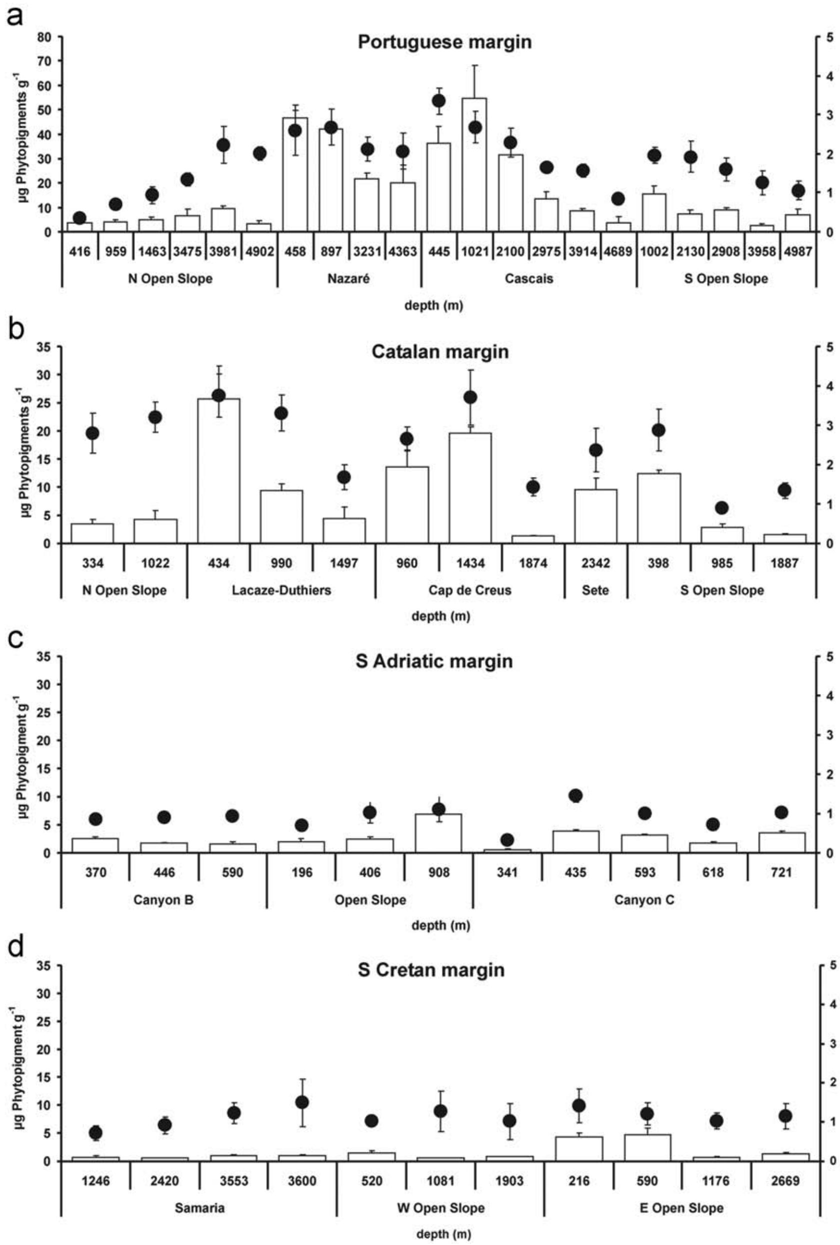

Fig. 4. Phytopigment and biopolymeric C contents in the sediment of all of the 55 stations along the Portuguese, Catalan, South Adriatic and South Cretan margins. Illustrated are values (± standard deviation of $n=3$ replicates) from the four investigated areas, divided by open slope and canyon settings 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			
	Catalan margin							
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			
	S Adriatic margin							
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			
	S Cretan margin							
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).

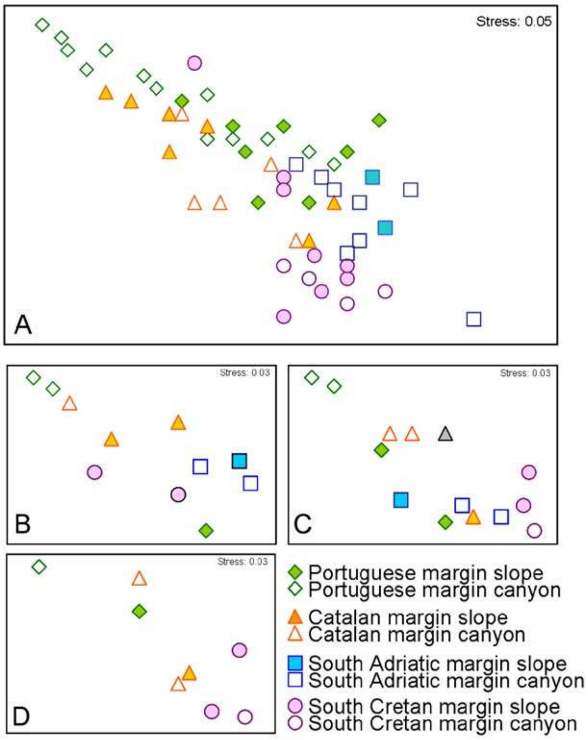

Fig. 5. nMDS ordination plots based on organic matter sedimentary contents showing the similarity among the different topographic features and different areas. Illustrated are regional patterns irrespective of depth (A), at 500 (B), 1000 (C) and 2000 (D) m depth. In panel (A) the arrows and percentage 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 (%)
Portuguese vs. Catalan	0.06	*	42.61	**Phytopigments**	70.81	70.82
				Carbohydrates	10.22	81.03
				Biopolymeric C	8.83	89.83
				Proteins	7.41	97.15
Portuguese vs. S Adriatic	0.29	***	51.42	**Phytopigments**	75.83	75.84
				Carbohydrates	7.82	83.63
				Biopolymeric C	7.31	90.92
Portuguese vs. S Cretan	0.41	***	56.23	**Phytopigments**	77.11	77.11
				Proteins	7.71	84.83
				Carbohydrates	6.93	91.73
Catalan vs. S Adriatic	0.39	***	48.23	**Phytopigments**	52.74	52.74
				Carbohydrates	17.04	69.75
				Biopolymeric C	14.62	84.33
				Proteins	11.65	95.92
Catalan vs. S Cretan	0.39	***	49.53	**Phytopigments**	59.24	59.22
				Proteins	13.93	73.12
				Biopolymeric C	12.31	85.43
				Carbohydrates	10.92	96.32
S Adriatic vs. S Cretan	0.32	***	39.72	**Phytopigments**	52.74	52.71
				Carbohydrates	20.12	72.82
				Proteins	12.11	84.91
				Biopolymeric C	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 (***=$P<0.001$; *=$P<0.05$).

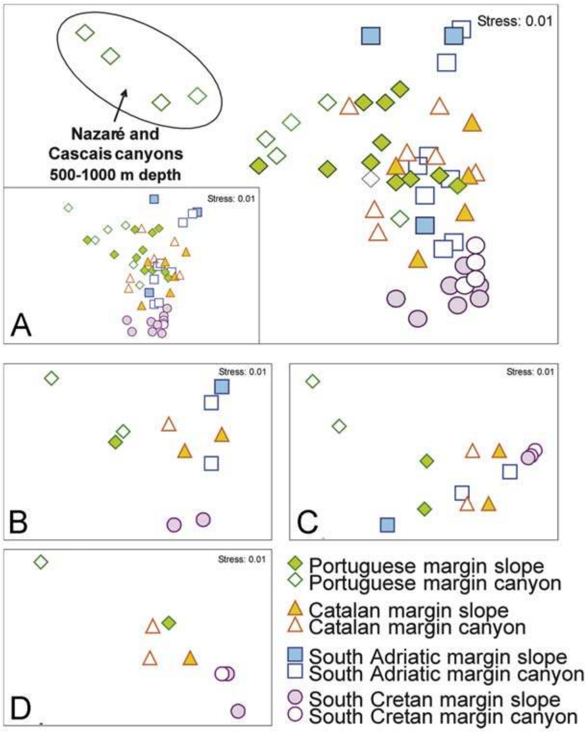

Fig. 6. nMDS ordination plot based on organic matter sediment bioavailability showing the similarity among the different topographic features and different areas. Illustrated are regional patterns irrespective of depth (A; the small left panel illustrates the nMDS output after the removal of data from 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 characterised by high primary production levels at the surface exhibit deep-sea sediment organic matter concentrations that are considerably higher than in oligotrophic oceanic regions (Tselepides 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-

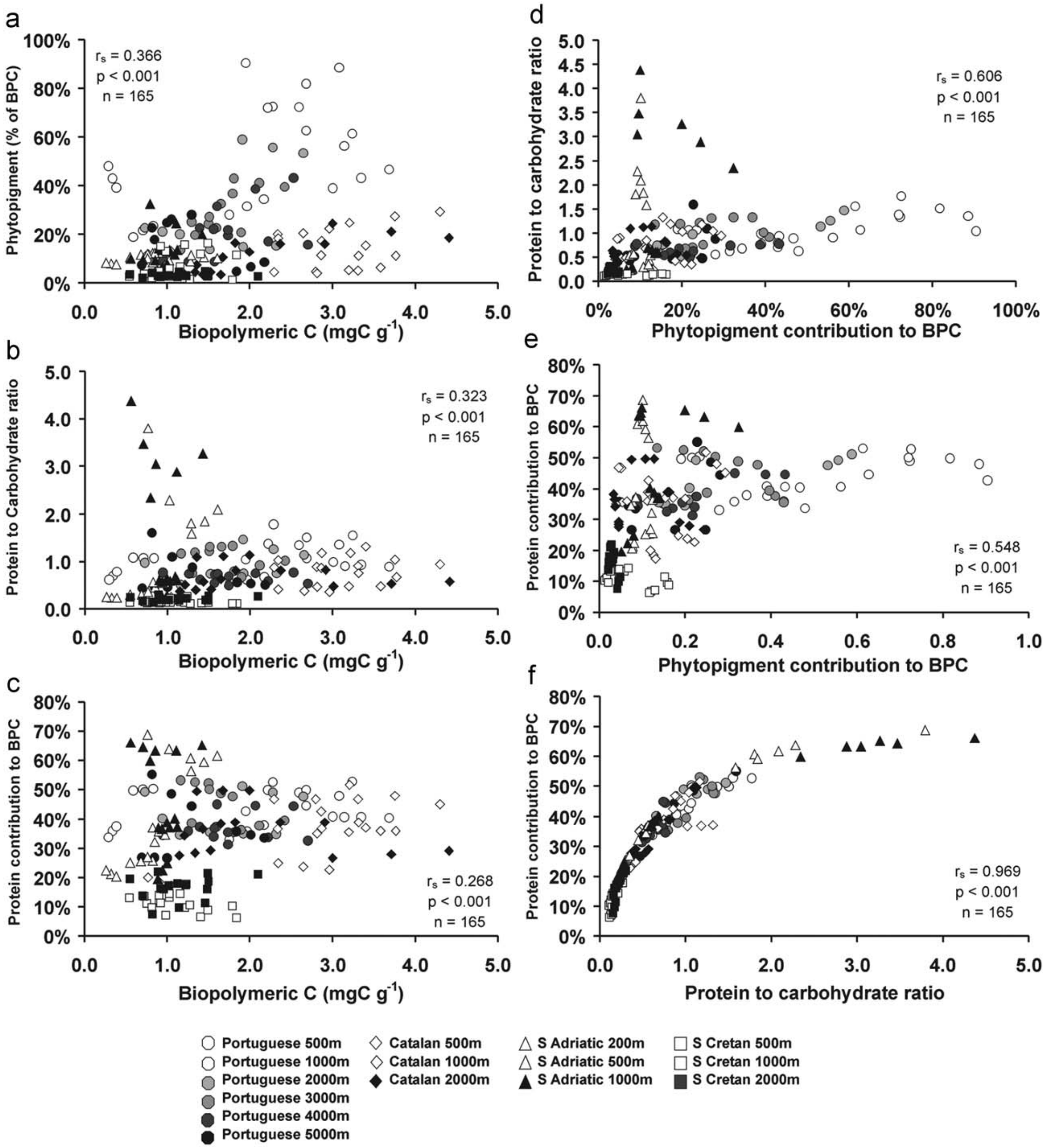

Fig. 7. Relationships between biopolymeric C concentrations and the protein contribution to biopolymeric C (a), the protein to carbohydrate ratio (b), the protein C contribution to biopolymeric C and the relationships between the phytopigment contribution to biopolymeric C and the protein to carbohydrate 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 (***=$P<0.001$; 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 (Moràn 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 (%)
A	**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	**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
C	**% 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 (%)
Portuguese margin	**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
Catalan margin	**% Sand**	1872.70	19.00	***	35.85	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
S Adriatic margin	**% 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
S Cretan margin	**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

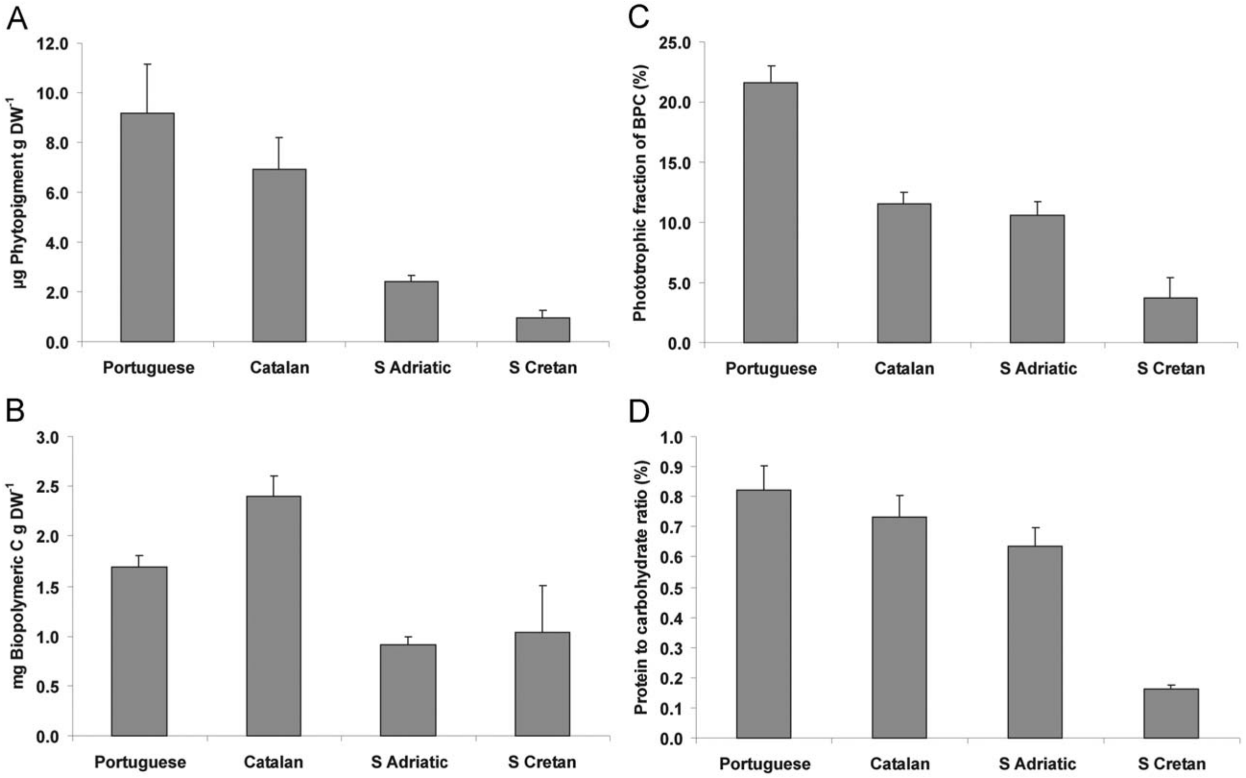

Fig. 8. Longitudinal patterns of quantity and nutritional quality of organic matter in the deep-sea sediments of the NE Atlantic and the Mediterranean Sea. The four different panels illustrate median concentrations (± standard errors) calculated from all stations belonging to the same area of: (A) phytopigment, (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 $\sim 64.5\,\mathrm{g\,m^{-2}\,d^{-1}}$ in the Portuguese margin (de Stigter et al., 2007), to 4–$12.5\,\mathrm{g\,m^{-2}\,d^{-1}}$ in the Gulf of Lions (Accornero et al., 2003), 1.7–$8.1\,\mathrm{g\,m^{-2}\,d^{-1}}$ in the South Adriatic margin (Turchetto et al., 2007) and 0.2–$0.5\,\mathrm{g\,m^{-2}\,d^{-1}}$ 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).

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