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Major consequences of an intense dense shelf water cascading event on deep-sea benthic trophic conditions and meiofaunal biodiversity

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Abstract. Numerous submarine canyons around the world are preferential conduits for episodic dense shelf water cascading (DSWC), which quickly modifies physical and chemical ambient conditions while transporting large amounts of material towards the base of slope and basin. Observations conducted during the last 20 yr in the Lacaze-Duthiers and Cap de Creus canyons (Gulf of Lion, NW Mediterranean Sea) report several intense DSWC events. The effects of DSWC on deep-sea ecosystems are almost unknown. To investigate the effects of these episodic events, we analysed changes in the meiofaunal biodiversity inside and outside the canyon. Sediment samples were collected at depths varying from ca. 1000 to > 2100 m in May 2004 (before a major event), April 2005 (during a major cascading event) and in October 2005, August 2006, April 2008 and April 2009 (after a major event). We report here that the late winter–early spring 2005 cascading led to a reduction of the organic matter contents in canyon floor sediments down to 1800 m depth, whereas surface sediments at about 2200 m depth showed an increase. Our findings suggest that the nutritional material removed from the shallower continental shelf, canyon floor and flanks, and also the adjacent open slope was rapidly transported to the deep margin. During the cascading event the meiofaunal abundance and biodiversity in the studied deep-sea sediments were significantly lower than after the event. Benthic assemblages during the cascading were significantly different from those in all other sampling periods in both the canyon and deep margin. After only six months from the cessation of the cascading, benthic assemblages in the impacted sediments were again similar to those observed in other sampling periods, thus illustrating a quick recovery. Since the present climate change is expected to increase the intensity and frequency of these episodic events, we anticipate that they will increasingly affect benthic bathyal ecosystems, which may eventually challenge their resilience.

1   Introduction

Dense shelf water cascading (DSWC) is a specific type of buoyancy driven current (Shapiro et al., 2003) which occurs when dense water forms over the continental shelf by cooling and/or by an increase in salt content of the coastal waters due to atmospheric forcing. When the dense waters overflow the shelf edge, they descend down the continental slope, until they reach the corresponding matching density. Suspended sediment concentration in the dense water plume also contributes to the excess density, and affects the dynamics of the plume by enhancing its equilibrium depth (Fohrmann et al., 1998). Major DSWC possibly contributes to the ventilation of deep waters (Killworth, 1977), and leads to large

suspended particle and organic matter fluxes (Heussner et al., 2006; Sanchez-Vidal et al., 2009).

DSWCs have been observed in many areas around the world, pre-eminently at mid- and high latitudes, and, more rarely, in tropical and subtropical regions (Ivanov et al., 2004; Durrieu de Madron et al., 2005; Canals et al., 2009).

Continental margins represent approximately 20 % of the world ocean's surface and play an important role in the biogeochemical cycles at the global scale (Walsh, 1991). Continental margins are characterized by the presence of different morphological characteristics of the sea bottom that include open slopes of variable steepness, submarine canyons and landslide-affected areas (Weaver et al., 2004). Submarine canyons dissect most margins of the world's continents (Harris and Whiteway, 2011). Some canyons have the head very close to the shoreline (Amblàs et al., 2006). The topographic and hydrodynamic features of some submarine canyons make these sites of intense exchange between the continental shelf and the deep margin and basin (Nittrouer and Wright, 1994), by intercepting and trapping coastal sediment drifts and driving the collected material towards the deep (Lewis and Barnes, 1999; Schmidt et al., 2001; Palanques et al., 2005; Flexas et al., 2002, 2008; Heussner et al., 2006). Canyons can favour or even amplify the effects of DSWC (Allen and Durrieu de Madron, 2009). Therefore, it has been hypothesized that DSWC could have a great influence on the biodiversity and functioning of canyon ecosystems and the deep margins and basins (Buscail and Germain, 1997; Etcheber et al., 1999; Martin et al., 2006; Skliris and Djenidi, 2006; Durrieu de Madron et al., 2000; Duineveld et al., 2001; Bianchelli et al., 2008; Company et al., 2008).

The long-term monitoring taking place since 1993 in the Lacaze-Duthiers Canyon shows that three extreme cascading events reaching at least 1000 m depth occurred in 1999, 2005 and 2006 (Heussner et al., 2006; Canals et al., 2006; Palanques et al., 2012). In particular, during the winters 2005 and 2006, major DSWC events, driven by exceptionally strong and dry northern winds, were observed along the Gulf of Lions and spread down to the deep margin with maximum bottom current velocities nearing $1 \, \mathrm{m \, s^{-1}}$ (Canals et al., 2006; Palanques et al., 2012). They conveyed large amounts of fresh organic material, due to the phytoplankton bloom occurring concomitantly on the shelf together with more detrital material from the resuspended sediment throughout the Lacaze-Duthiers and Cap de Creus canyons at the southwestern end of the gulf (Canals et al., 2006; Sanchez-Vidal et al., 2009).

In the present study we tested the hypothesis that the DSWC event that occurred in early 2005 affected the biodiversity of the deep-sea benthic ecosystems. We accordingly investigated the differences in meiofaunal biodiversity and trophic conditions inside and outside the Cap de Creus Canyon (CCC), over a period of six years, before, during and after these major DSWC events.

2 Materials and methods

2.1 Study area and characteristics of the cascading event

The Gulf of Lions is one of the Mediterranean Sea regions characterized by the most intricate network of submarine canyons with heads cut into the 130 m-deep crescent-shaped shelf (Canals et al., 2006). Some canyons extend for more than 100 km, cutting the entire continental slope and reaching depths > 2000 m (Amblàs et al., 2006; Canals et al., 2009). Among these, the CCC, incising the western Gulf of Lions continental shelf and slope, converges into the larger Sète Canyon (Lastras et al., 2007).

During late winter–early spring 2005, a particularly intense dense shelf water cascading (DSWC) occurred, triggered by abnormally cold, strong and persistent northern winds, and by lower-than-average freshwater inputs from rivers entering the gulf. Dense waters overflowed the shelf edge and, flowing along the continental slope over the bottom, reached the lower continental slope and basin at depths > 2000 m (Canals et al., 2006).

In the CCC, the event was recorded as a sudden drop in deep-sea temperature (by up to about 3.0 °C at 750 m depth), increased down-canyon current speed (up to > $1 \, \mathrm{m \, s^{-1}}$) and water density, and caused a cumulative sediment transport with fluxes up to $3 \, \mathrm{t \, m^{-2}}$ for the 3-day-long strongest flushing outburst in late February (Canals et al., 2006). The organic carbon (OC) export associated with this event was estimated to be more than half a million tons (an average of about $15000 \, \mathrm{t \, d^{-1}}$ for the entire duration of the cascading event; Canals et al., 2006).

2.2 Sampling

Sediment sampling was carried out along the major axis of the CCC in the Gulf of Lions and in the deep margin during different oceanographic cruises carried out before (May 2004), during (April 2005) and after (October 2005, August 2006, April 2008 and 2009) the winter 2005 DSWC event (Fig. 1). Samples for the analysis of the quantity and bioavailability of sedimentary organic matter (OM) were collected at from ca. 1000 m and ca. 1800 m depth along the major axis of the Cap de Creus Canyon, and at > 2100 m depth on the deep margin where the Cap de Creus and the Sète canyons merge. For ease of clarity, the deepest station will be referred to as "deep margin" from here onwards.

Sediment samples for the analysis of meiofaunal and nematode biodiversity were retrieved at ca. 1000 and ca. 1800 m depth at all sampling dates, except May 2004. Additional samples for the meiofaunal analyses were collected at > 2100 m depth in April 2005, October 2005, August 2006 and April 2009. Sampling time, latitude, longitude and depth of all sampling stations are reported in Table 1.
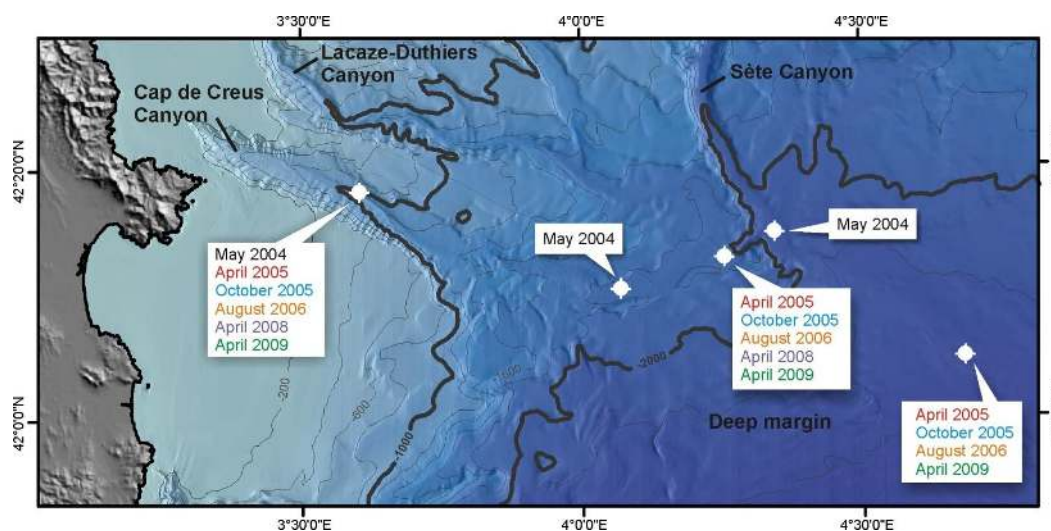
Fig. 1. Location of sampling areas in the Cap de Creus Canyon and the deep margin. Dots include neighboring stations visited during different sampling periods. Geographical coordinates of sampling stations are detailed in Table 1.

Table 1. Location and depth of sampling stations in the Cap de Creus Canyon and deep margin.

Date	Area	Depth (m)	Latitude (N)	Longitude (E)
May 2004	Cap de Creus	940	42°18.4′	3°35.5′
	Cap de Creus	1801	42°10.4′	4°04.2′
	Deep margin	2112	42°14.9′	4°20.7′
Apr 2005	Cap de Creus	960	42°18.5′	3°36.0′
	Cap de Creus	1874	42°12.9′	4°15.3′
	Deep margin	2342	42°04.8′	4°40.5′
Oct 2005	Cap de Creus	960	42°18.5′	3°36.0′
	Cap de Creus	1874	42°12.9′	4°15.3′
	Deep margin	2342	42°04.8′	4°40.5′
Aug 2006	Cap de Creus	960	42°18.5′	3°36. 0′
	Cap de Creus	1870	42°12.9′	4°15.4′
	Deep margin	2340	42°04.8′	4°40.1′
Apr 2008	Cap de Creus	1000	42°18.5′	3°36.7′
	Cap de Creus	1800	42°12.9′	4°15.4′
	Deep margin	–	–	–
Apr 2009	Cap de Creus	983	42°18.2′	3°37.0′
	Cap de Creus	1845	42°12.9′	4°15.4′
	Deep margin	2320	42°04.9′	4°42.0′

At all sites, replicate sediment samples were collected using a NIOZ-type box corer (May 2005, April 2005) or an OCTOPUS multi-corer (October 2005, August 2006, April 2008, April 2009), allowing the collection of undisturbed sediment samples. At each station, the top 1 cm of three sediment cores (internal diameter 3.6 cm), each obtained from independent deployments of the box or multicorer, was analyzed for meiofaunal community structure, nematode species richness, and OM biochemical composition.

Sediment samples for the faunal analyses were preserved with formalin (4 % in sea water), after staining with a few drops of Rose Bengal. Sediment samples for the biochemical analyses were stored at −20 °C until analysis in the laboratory.

2.3 Quantity and biochemical composition of sedimentary organic matter

Total protein and carbohydrate sediment contents were determined spectrophotometrically and concentrations expressed as bovine serum albumin and glucose equivalents, respectively (Danovaro, 2010). For each biochemical assay, blanks were obtained using pre-combusted sediments (450 °C for 4 h). All analyses were performed on triplicate superficial (0–1 cm) sediment samples (about 0.5 g). The total pools of protein and carbohydrate include both refractory and labile components. The labile (bioavailable) components of the protein and carbohydrate pools were determined after enzymatic hydrolysis of the sediment, according to Dell'Anno et al. (2000).

Frozen sediment samples were homogenized in TRIS-HCl 0.1 M, EDTA 0.1 M buffer (pH 7.5, buffer volume : sediment weight ratio of 2.5) and the resulting slurry sonicated three times for 1 min (with intervals of 30 s every minute). Triplicate subsamples of the slurry (treated samples) were added to 100 μL of proteinase K (1 mg mL^{-1}), and 100 μL of protease (600 μg mL^{-1}) solutions. An equal volume of TRIS-HCl 0.1 M, EDTA 0.1 M buffer solution without enzymes (control samples) was added to another set of triplicate sediment subsamples. All subsamples were incubated for 1 h at 37 °C under gentle agitation, filtered onto GF/F filters and rinsed twice with 5 mL of cold reagent grade water to remove the digested proteins and the remaining enzymes. Sediment subsamples (0.1 g) muffled at 450 °C for 4 h and processed as describe above were utilized as blanks. Protein analyses

from these samples were then carried out spectrophotometri-cally (Danovaro, 2010). Differences between protein concentration of control and treated samples were assumed to account for the proteins actually hydrolyzed by proteases (hydrolyzed proteins). Hydrolyzed protein concentrations were normalized to sediment dry weight.

For enzymatic digestion of carbohydrates, frozen sediment samples were homogenized with 0.1 M Na-phosphate, 0.1 M EDTA (pH 5.0; buffer volume : sediment weight ratio of 2.5) and sonicated three times for 1 min (with intervals of 30 s every minute). Triplicate subsamples of the slurry (treated samples) were added to 100 μL of α-amylase, 50 μL of β-glucosidase, 100 μL of proteinase K and 100 μL of lipase (stock solution of all enzymes was 1 mg mL^{-1}). Another set of slurry subsamples added to 0.1 M Na-phosphate instead of the aforementioned enzymes was utilized as control. Samples were incubated for 1 h at room temperature under gentle agitation as for protein hydrolysis. Sediment subsamples, muffled at 450 °C for 4 h and processed as described above, were utilized as blanks. After incubation, all samples were centrifuged at 2000 × g for 10 min and an aliquot of the supernatant was utilized to determine carbohydrates released from the sediments. Soluble carbohydrates were determined from the supernatant of the control sample. Carbohydrates from the supernatant and intact sediments were analyzed spectrophotometrically (Danovaro, 2010). The actual fraction of enzymatically hydrolyzed carbohydrates was obtained by difference between the carbohydrate concentrations determined in the supernatant of samples containing enzymes and in the soluble fraction of the control. Hydrolyzed carbohydrate concentrations were normalized to sediment dry weight.

Total and enzymatically hydrolyzed carbohydrate and protein sedimentary contents were converted into carbon equivalents using the conversion factors of 0.40 and 0.49 mg C mg^{-1}, respectively. Generally, biopolymeric C (BPC) is defined as the sum of total protein, carbohydrate and lipid sedimentary contents (Pusceddu et al., 2009). In this, study, however, the biopolymeric C includes only total proteins and carbohydrates, whereas the concentrations of their respective enzymatically hydrolysable (bioavailable) fractions are summed up and thereafter reported as bioavailable organic C (Danovaro et al., 2001; Pusceddu et al., 2003; Dell'Anno et al., 2013). The percentage of bioavailable over biopolymeric C is defined as the bioavailable fraction of BPC.

2.4 Meiofauna and nematode biodiversity

For the meiofaunal analyses, the sediment samples had been sieved through a 1000 μm mesh, with a 20 μm mesh then used to retain the smallest organisms. The fraction remaining on the 20 μm sieve was re-suspended and washed three times (800 × g, 10 min, room temperature) in Ludox HS40 colloidal silica (density, 1.31 g cm^{-3}) (Danovaro, 2010). All

animals that remained in the supernatant were again passed through a 20 μm mesh net, washed with tap water, stained with 0.5 g L^{-1} Rose Bengal solution, and sorted under a stereomicroscope (magnification, 40X). Meiofaunal biomass was assessed by bio-volumetric measurements for all specimens encountered, according to Danovaro (2010).

For the nematode diversity analysis, 100 randomly chosen nematodes from each of the three replicates (or all of the nematodes when the abundance was lower than 100 specimens per sample) were mounted on slides, following the formalin-ethanol-glycerol technique to prevent dehydration (Seinhorst, 1959; Heip et al., 1985; Danovaro, 2010). The nematodes were identified to species level according to the presently used manuals (Platt and Warwick, 1983, 1988; Warwick et al., 1998; Deprez et al., 2005). All unknown species were recorded as sp$_1$, sp$_2$, sp$_3$, …, sp$_n$.

The nematode diversity was estimated using the species richness (SR) as the total number of different species identified in each sample. Each replicate sampling from each area was analyzed separately; the biodiversity at each area was determined cumulatively as the total number of different species retrieved from the three independent replicates. As species richness is strongly affected by sample size, the expected number of species, ES, was also estimated, which provides a standardization of the values of the species richness according to the sample size. At each site, the expected number of species for a theoretical sample of 100 specimens, ES$_{(100)}$, was chosen and calculated cumulatively as the total number of expected species retrieved from the three replicates. The species diversity (H', using log-base 2, expressed as H') was also measured by the Shannon–Wiener index. These indices were calculated from the sum of the individuals of the three cores from each of the sampling sites, using PRIMER v6.0+ (Plymouth Marine Laboratory, UK; Clarke and Gorley, 2006). We also measured the turnover diversities (β-diversity) between sampling times, separately for the different depth ranges, using the similarity percentage analysis (SIMPER) routine that is included in the PRIMER v6.0+ software. Turnover diversity among samling times is reported as the percentage dissimilarity calculated from resemblance matrixes based on Bray–Curtis dissimilarity after transformation of the raw data into presence/absence matrixes.

2.5 Statistical analyses

To test the ecosystem response to the DSWC, we used both uni- and multivariate permutational non-parametric analyses of variance (PERMANOVA) (Anderson, 2001; McArdle and Anderson, 2001). We determined the effects of the cascading on each variable separately; the design included two orthogonal factors: sampling time (5–6 and 4–5 fixed levels for meiofauna and OM data in the canyon and the deep basin, respectively) and water depth (2 fixed levels: ca. 1000 m and ca. 1800 m depth), with $n = 3$ for the combination of factors. Since the information for the deep margin did not include

data from April 2008, to avoid unbalanced designs a separate one-way test (with sampling time as the unique source of variation with 4 fixed levels, April 2005, October 2005, August 2006 and April 2009) was carried out to ascertain the effects of cascading at > 2100 m depth in the deep margin. Since most time $\times$ depth interactions were found to be significant, pairwise comparison tests were also carried out to discriminate the effects of the cascading, separately for the two different depths (Tables S1 and S2 in Supplement). PERMANOVA was also used to test the effects of the cascading on the meiofaunal community structure and the nematode assemblage composition. The results of the PERMANOVA have been illustrated as biplots produced after a canonical analysis of principal coordinates (CAP). The designs were the same as those adopted for the univariate tests, with the exclusion of the sampling carried out in May 2004, for which meiofaunal data were unavailable. The PERMANOVA tests were based on Euclidean distances of previously normalized data (OM data) or Bray–Curtis similarity matrixes (after presence/absence transformation of the data), using 4999 random permutations of the appropriate units (Anderson and ter Braak, 2003). Univariate tests were carried out using unrestricted permutation of the raw data, whereas multivariate analyses were carried out with permutation of residuals under a reduced model. SIMPER analyses were also carried out to estimate the turnover of nematode diversity between sampling times and depths. SIMPER, uni- and multivariate PERMANOVA tests and CAP analysis were carried out using the PERMANOVA and SIMPER routines included in the PRIMER6+ software.

3   Results

3.1   DSWC effects on sediment organic matter quantity and composition

PERMANOVA results for the effects of DSWC in the CCC (at ca. 1000 and ca. 1800 m depth) and in the deep margin (at > 2100 m depth) on the sedimentary OM contents and the bioavailable fraction of biopolymeric C (BPC) are reported in Table 2. These analyses, carried out separately for the CCC and the deep margin (at ca. 2200 m depth), reveal a consistently significant effect of the time $\times$ depth interaction for all the investigated variables. The results of pairwise comparisons (Table S1 in Supplement) reveal that the differences among the concentrations of BPC in sediments collected during the cascading and during all other sampling dates, although often significant, are not always consistent. For example, at ca. 1000 and ca. 1800 m depth in the CCC, the concentrations of BPC during the cascade are lower than those measured in the previous period (May 2004), but similar to or higher than those observed in equivalent sampling periods and depths but in the following years (i.e. April 2008 and April 2009) characterized by the absence of cascading
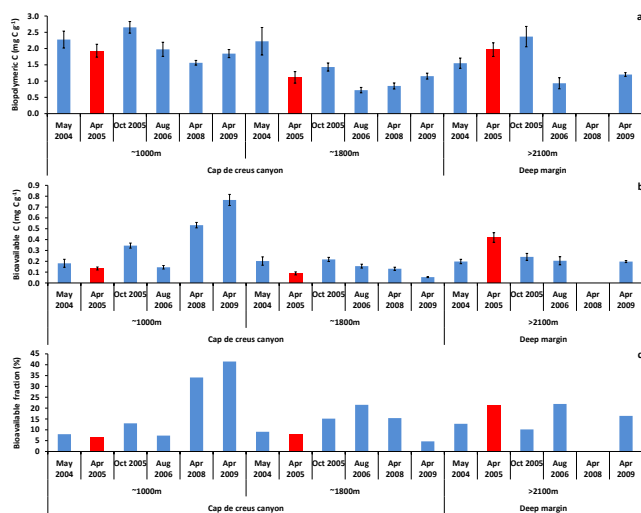
Fig. 2. Spatial and temporal variation in the sedimentary contents of biopolymeric C **(a)**, bioavailable C **(b)** and the bioavailable fraction of BPC **(c)** in the Cap de Creus Canyon and in the deep margin. Red bars indicate DSWC.

(Fig. 2a). In the deep margin BPC concentrations during the cascade are significantly higher than those observed before (May 2004) or after (April 2009) the cascading. On the other hand, the pairwise comparisons (Table S1 in Supplement) reveal that the sedimentary concentrations of bioavailable C and the values of the bioavailable fraction (%) of biopolymeric C at both depths in the Cap de Creus during the cascading (April 2005) are significantly and consistently lower than those measured either before (May 2004) or after the cascading (with the exception of August 2006; Fig. 2a–b). In the sediments of the deep margin, the sedimentary contents of bioavailable C and the values of the bioavailable fraction of BPC during the cascading are consistently and significantly higher than those measured either before or after the cascading (Fig. 2b–c).

3.2   DSWC effects on meiofaunal abundance and biomass

At all sampling depths in both the CCC and deep margin, meiofaunal abundances during the cascading event (April 2005) are significantly lower than after the DSWC event (Tables 3 and Table S2 in Supplement) (Fig. 3a). Similar differences, with a few exceptions (Table S2 in Supplement), are observed also for meiofaunal biomass (Fig. 3b). A few months after the cascading (e.g. in October 2005), at all depths, meiofaunal abundance and biomass display values similar to those observed in all other sampling periods, with the exception of April 2008 for meiofaunal biomass (Fig. 3a–b).

Table 2. Results of the PERMANOVA tests on the quantity and bioavailability of biopolymeric C in the sediments of the Cap de Creus Canyon and deep margin. Also reported is the percentage of variance explained by each source of variation and their interaction. df = degrees of freedom; MS = means square; F = statistic F; P = probability level. *** = $P < 0.001$; ** = $P < 0.01$.

Area	Variable	Source	df	MS	Pseudo F	P	% of explained variance
Canyon	Biopolymeric C	Time	5	2.64	20.06	***	26.6
		Depth	1	14.82	112.42	***	51.8
		Time × depth	5	0.76	5.76	**	13.3
		Residual	24	0.13			8.4
	Bioavailable C	Time	5	1.92	115.60	***	16.8
		Depth	1	9.57	576.74	***	28.1
		Time × depth	5	3.09	186.28	***	54.2
		Residual	24	0.02			0.9
	Bioavailable fraction	Time	5	2.43	123.24	***	21.4
		Depth	1	2.67	135.46	***	7.9
		Time × depth	5	3.94	199.44	***	69.6
		Residual	24	0.02			1.1
Deep margin	Biopolymeric C	Time	4	3.18	24.92	***	88.9
		Residual	10	0.13			11.1
	Bioavailable C	Time	4	3.21	27.62	**	89.9
		Residual	10	0.12			10.1
	Bioavailable fraction	Time	4	3.02	15.66	***	83.0
		Residual	10	0.19			17.0

Table 3. Results of the PERMANOVA tests on the abundance and biomass of meiofauna in the sediments of the Cap de Creus Canyon and deep margin. Also reported is the percentage of variance explained by each source of variation and their interaction. df = degrees of freedom; MS = means square; F = statistic F; P = probability level. *** = $P < 0.001$; ** = $P < 0.01$; * = $P < 0.05$, ns = not significant.

Area	Variable	Source	df	MS	Pseudo F	P	% of explained variance
Canyon	Meiofaunal abundance	Time	4	9.82	36.15	***	68.6
		Depth	1	1.41	5.19	*	4.1
		Time × depth	4	0.96	3.54	*	12.5
		Residual	20	0.27			14.8
	Meiofaunal biomass	Time	4	5.63	11.64	***	46.1
		Depth	1	4.51	9.33	**	14.4
		Time × depth	4	1.24	2.55	ns	13.5
		Residual	20	0.48			26.0
Deep margin	Meiofaunal abundance	Time	3	2.84	27.13	***	90.1
		Residual	8	0.10			9.9
	Meiofaunal biomass	Time	3	1.03	7.06	***	66.9
		Residual	8	0.15			33.1

3.3 DSWC effects on the richness of meiofaunal higher taxa and on nematode biodiversity

During the cascading, only one taxon (the nematodes) is encountered at both sampling depths in the CCC sediments and only 3 taxa (nematodes, copepods and polychaetes) were encountered in the deep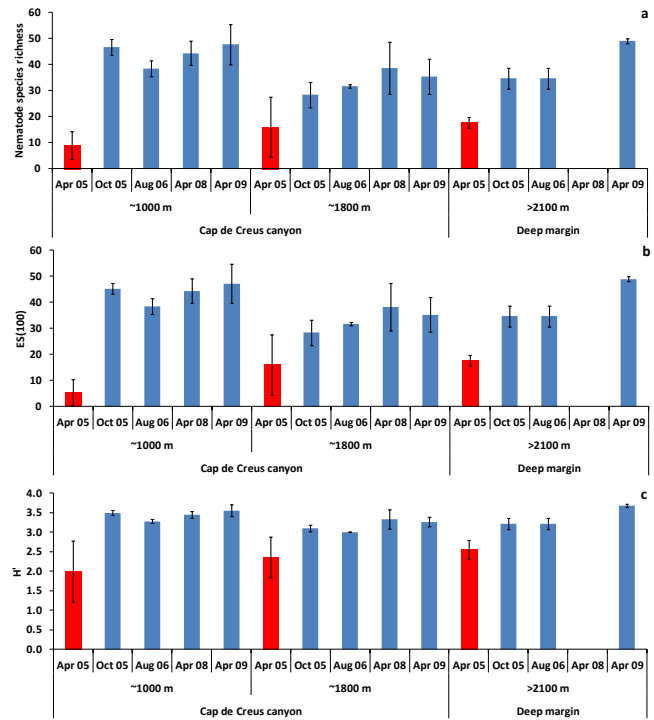 margin (Fig. 3c). For all other sampling periods, but April 2008 at ca. 1000 m depth, a total of 5-11 taxa are recorded within the CCC sediments and in the deep margin. The results of the PERMANOVA tests carried out on the nematode biodiversity separately for the CCC and the deep margin are reported in Table 4. During the cascading (April 2005), in both the CCC and deep margin, nematode biodiversity, expressed either as species richness, expected
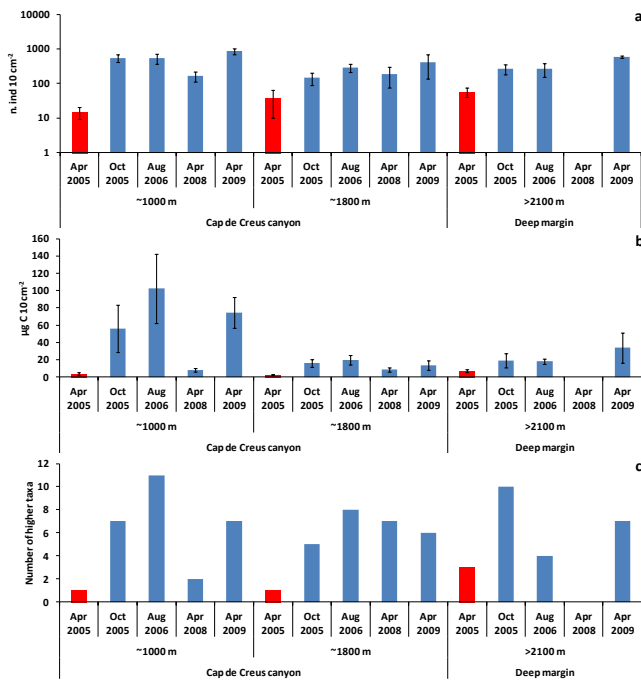
Fig. 3. Spatial and temporal variation in meiofaunal abundance **(a)**, biomass **(b)** and richness of higher taxa **(c)** in the Cap de Creus Canyon and deep margin. Red bars indicate DSWC.

Fig. 4. Spatial and temporal variation in nematode specie richness **(a)**, expected species number [$\text{ES}_{(100)}$] **(b)** and Shannon's H' values **(c)** in the Cap de Creus Canyon and deep margin. Red bars indicate DSWC.

species number [$\text{ES}_{(100)}$] or as Shannon's (H') index, is significantly lower (Table 4) than after the DSWC event (Fig. 4). The multivariate PERMANOVA tests reveal significant temporal variations in the composition of the nematode assemblages at all depths in both the Cap de Creus Canyon and deep margin (Table 5). The biplots produced after the CAP analysis, which identifies a clear and significant segregation of the different sampling periods (Table S3 in Supplement), show that the compositions of the nematode assemblages observed in canyon and deep margin sediments during the cascading are clearly different from those observed for all other sampling periods after cascading. (Fig. 5). In more detail, in the Cap de Creus, the dissimilarity among nematode assemblages observed during the 2005 DSWC event and those after the event (range 90–97 %) is larger than the dissimilarity among sampling periods not affected by cascading (range 76–86 %) (Fig. 5). In the deep margin the dissimilarity among nematode assemblage compositions during the DSWC and all other sampling periods (range 96–97 %) is barely higher than the one measured among assemblages observed after the cascading. The SIMPER analyses reveal also that different species contributed to the dissimilarity between the assemblages observed during the 2005 cascading event and those observed after the event (Table S4).

4 Discussion

Deep-sea biomes still form the least accessible and probably the least understood ecosystems of our planet. Recent innovations in remote sensing techniques allowed the discovery that deep-sea habitats are more complex, heterogeneous and dynamic than previously hypothesized. There is increasing evidence that the deep-sea habitats may respond quickly to shifts in upper-ocean variables occurring over medium (months) to long-term (years) temporal scales (Danovaro et al., 2004; Smith et al., 2009; Glover et al., 2010; Sanchez-Vidal et al., 2012; López-Fernández et al., 2012), as well as to a variety of anthropogenic stressors, from fisheries (e.g. Bailey et al., 2009; Puig et al., 2012) to pollution (Unger et al., 2008; Ramirez Llodra et al., 2012).

Deep-sea ecosystems respond rapidly to the seasonal primary productivity pulses leading to the exportation of OM from the upper ocean (Billet et al., 2001; Wigham et al., 2003). However, an increasing number of studies now documents atmosphere and climate-driven episodic events, that might favour the transfer of sedimentary OM from the upper part of the continental margin down to the deep margin and basin (Klein et al., 1999; Canals et al., 2006; Heussner et al., 2006; Sanchez-Vidal et al., 2008, 2009, 2012; Palanques et al., 2006, 2012; López-Fernández et al., 2012).

Table 4. Results of the PERMANOVA tests on nematodes biodiversity, estimated as species richness, expected species number (ES$_{(100)}$) and H' values in the sediments of the Cap de Creus Canyon and deep margin. Also reported is the percentage of variance explained by each source of variation and their interaction. df = degrees of freedom; MS = means square; F = statistic F; P = probability level. *** = $P < 0.001$; ** = $P < 0.01$; * = $P < 0.05$; ns = not significant.

| Area	Variable	Source	df	MS	Pseudo F	P	% of explained variance
Canyon	Specie richness	Time	4	880.80	20.45	***	59
		Depth	1	388.80	9.03	**	10
		Time × depth	4	132.97	3.09	*	13
		Residual	20	43.07			18
	ES$_{(100)}$	Time	4	977.85	24.39	***	62
		Depth	1	289.98	7.23	*	7
		Time × depth	4	162.16	4.04	*	16
		Residual	20	40.10			16
	H'	Time	4	1.61	16.01	***	69
		Depth	1	0.16	1.57	ns	1
		Time × depth	4	0.13	1.33	ns	3
		Residual	20	0.10			27
Deep margin	Specie richness	Time	3	492.67	51.86	***	94
		Residual	8	9.50			6
	ES$_{(100)}$	Time	3	490.37	51.59	***	94
		Residual	8	9.50			6
	H'	Time	3	0.64	24.36	***	89
		Residual	8	0.03			11

Table 5. Results of the PERMANOVA tests on nematode assemblage compositions in the sediments of the Cap de Creus Canyon and deep margin. Also reported is the percentage of variance explained by each source of variation and their interaction. df = degrees of freedom; MS = means square; F = statistic F; P = probability level. *** = $P < 0.001$; ** = $P < 0.01$; * = $P < 0.05$; ns = not significant.

Area	Source	df	MS	Pseudo F	P	% of explained variance
Canyon	Time	4	11229	59.35	***	40
	Depth	1	3535	18.68	*	3
	Time × depth	4	2998	15.84	**	9
	Residual	20	1892			48
Deep margin	Time	3	7921	48.65	***	56
	Residual	8	1628			44

The DSWC events in late winter–early spring 2005 and 2006 are among the most intensive events ever recorded along the north Catalan margin, which transported huge amounts of material down to the deep margin through the CCC (Canals et al., 2006; Palanques et al., 2012). We show here that the 2005 event had a major impact on the trophic conditions of the deep-sea ecosystem and was associated with major changes in the biodiversity of meiofauna. Unfortunately, having no benthic data available for the 2006 cascading event (i.e. April 2006), we cannot infer further on this event also. During the 2005 cascading event, deep-sea currents (up to $> 1\,\mathrm{m\,s^{-1}}$) resulted in the flushing of huge amounts of labile organic material from the upper part of the canyon to the deep margin and basin. Although a positive response of benthic organisms could have been expected, we observed that the abundance, biomass, richness of meiofaunal higher taxa and nematode biodiversity during the cascading were generally much lower than after the DSWC event. At all depths, these variables, indeed, were up to one order of magnitude lower than those observed in post-cascading periods. The low values of meiofaunal abundance, biomass and biodiversity along the canyon can be due to the hydrodynamic stress that resuspended and dispersed the surface sediment layer during the cascading (Canals et al., 2006),
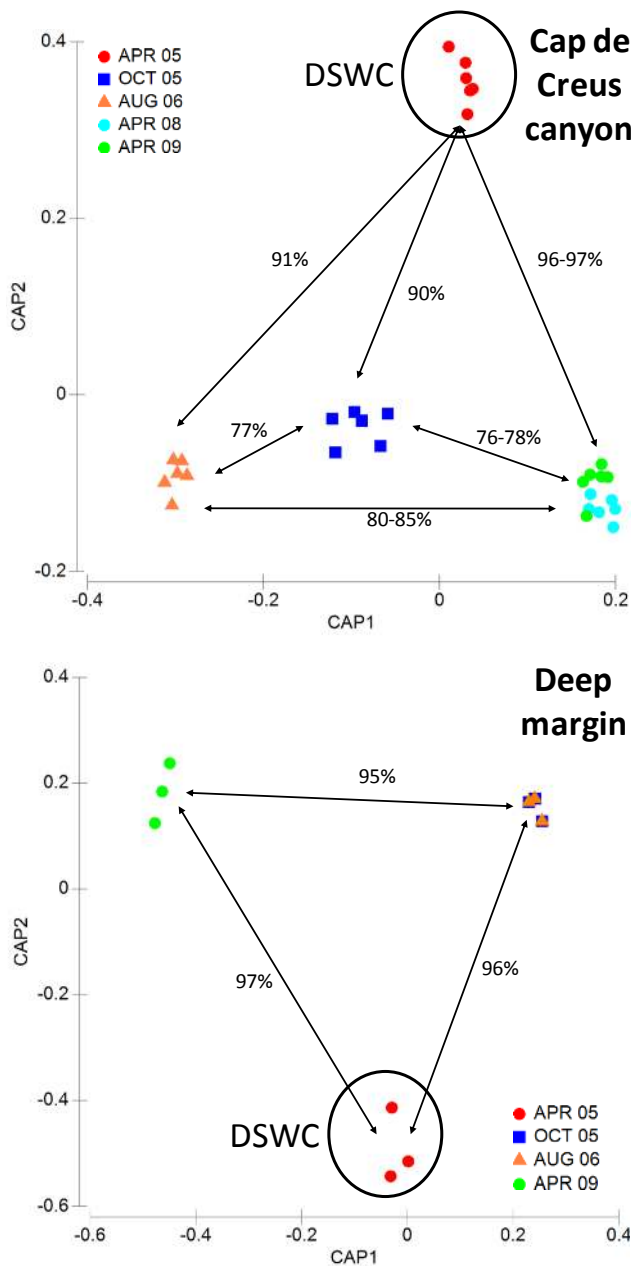
Fig. 5. Biplot after canonical analysis of principal coordinates illustrating temporal variability in the composition of nematode assemblages in the Cap de Creus Canyon (upper panel) and deep margin (lower panel). Also reported is the percentage of dissimilarity among nematode assemblages in different sampling times, calculated after SIMPER analysis. Red bars indicate DSWC.

whereas the low values in the deep margin meiofauna could be the result of suffocation due to the massive deposition of sediments transported by the cascading to the distal part of the canyon. Accordingly, the compositions of the nematode assemblages during the cascading were very different from those in post-cascading conditions at all depths. Previous studies conducted in different deep-sea canyons reported

significantly negative correlations between biodiversity and OC concentrations (Cunha et al., 2011; Vetter and Dayton, 1999), which were hypothesized to represent the descending portion of the unimodal relationship between diversity and food availability. Our results suggest that the low values of meiofaunal abundance and diversity during the 2005 cascading event are mostly likely an effect of the massive disturbance caused by cascading flows rather than controlled by an increased food availability. Moreover, the results of the SIMPER analyses show that different groups of nematode species explained the dissimilarity between assemblages during and after the 2005 cascading event at the different depth ranges. This result suggests that species encountered in DSWC-impacted sediments were random survivors, and the 2005 cascading event massively hit the benthos leaving no room for any possible selection of specifically resistant species and possibly leading to random local extinctions.

After the cessation of the cascading, we observed a fast recovery of deep-sea meiofaunal assemblages. Six months after the event, meiofaunal abundance, biodiversity and community composition recovered to values typically observed in all other sampling periods. The apparent quick recovery of the deep-sea assemblages after cascading can be explained by the high turnover (up to > 10 generations yr^{-1}) and opportunistic life strategies of meiofauna. Also, the increased food availability observed in the deep margin and the ecological space released by the meiofauna killed or brought away by cascading could have favoured the fast recovery of meiofaunal assemblages. Based on these results, we could infer that the impact of DSWC on the deep-sea meiofauna had a limited temporal effect. A similar temporally limited effect has been reported from the analysis of the highly valued deep-sea shrimp *Aristeus antennatus* recruitment and catch, which were abated by the cascading and showed a strong recovery after the cessation of the episodic event (Company et al., 2008).

Besides the evidence provided in this study, we must consider also that, for the deep margin (> 2100 m depth), open-sea convection can also be a concurrent causative agent of the observed variations after cascading (Stabholz et al., 2013). Strong near-bottom particle flux, due partly to local sediment resuspension by strong currents that occurred during bottom-reaching convection (like in 2005 and, possibly, 2006), are associated to the DSWC plume spreading. For milder winters (like in 2007 and 2008), the open-sea convection did not reach the bottom and thus had possibly only little impacts on bathyal ecosystems.

Climate change is unequally impacting marine ecosystems in different regions. The Mediterranean Sea is one of the marine systems in the world more sensitive to the effects of climate change (Canals and Ballesteros, 2009; Philippart et al., 2011). The on-going climate change is expected to increase the intensity and frequency of episodic events in the Mediterranean Sea and in other mid- and high latitude regions of the world (Somot et al., 2006; Coma et al., 2009;

Thomsen et al., 2012), and we anticipate that benthic bathyal ecosystems will be increasingly impacted by them in the future, which may eventually challenge their resilience.

Supplementary material related to this article is available online at: http://www.biogeosciences.net/10/ 2659/2013/bg-10-2659-2013-supplement.pdf.

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