



# Organic matter pools, C turnover and meiofaunal biodiversity in the sediments of the western Spitsbergen deep continental margin, Svalbard Archipelago

A. Pusceddu, L. Carugati, C. Gambi, J. Mienert, B. Petani, A. Sanchez-Vidal, M. Canals, S. Heussner, R. Danovaro

## ► To cite this version:

A. Pusceddu, L. Carugati, C. Gambi, J. Mienert, B. Petani, et al.. Organic matter pools, C turnover and meiofaunal biodiversity in the sediments of the western Spitsbergen deep continental margin, Svalbard Archipelago. Deep Sea Research Part I: Oceanographic Research Papers, 2016, 107, pp.48-58. 10.1016/j.dsr.2015.11.004 . hal-01273257

**HAL Id: hal-01273257**

**<https://univ-perp.hal.science/hal-01273257>**

Submitted on 15 Aug 2022

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License

# Organic matter pools, C turnover and meiofaunal biodiversity in the sediments of the western Spitsbergen deep continental margin, Svalbard Archipelago

A. Pusceddu <sup>a,\*</sup>, L. Carugati <sup>a</sup>, C. Gambi <sup>a</sup>, J. Mienert <sup>b</sup>, B. Petani <sup>a</sup>, A. Sanchez-Vidal <sup>c</sup>, M. Canals <sup>c</sup>, S. Heussner <sup>d</sup>, R. Danovaro <sup>a,e</sup>

<sup>a</sup> Dipartimento di Scienze della Vita e dell'Ambiente, Università degli Studi di Cagliari, Via T. Fiorelli 1, 09126 Cagliari, Italia

<sup>b</sup> The Arctic University of Norway, Tromsø, Norway

<sup>c</sup> GRC Geociències Marines, Departament d'Estratigrafia, Paleontologia i Geociències Marines, Universitat de Barcelona, Barcelona, Spain

<sup>d</sup> CEFREM, UMR CNRS 5110, CNRS-Univ. Perpignan, Perpignan, France

<sup>e</sup> Stazione Zoologica Anton Dohrn, Villa Comunale I, Napoli, Italia

We investigated organic matter (OM) quantity, nutritional quality and degradation rates, as well as abundance and biodiversity of meiofauna and nematodes along the deep continental margin off Spits-bergen, in the Svalbard Archipelago. Sediment samples were collected in July 2010 and 2011 along a bathymetric gradient between 600 m and 2000 m depth, and total mass flux measured at the same depths from July 2010 to July 2011. In both sampling periods sedimentary OM contents and C degradation rates increased significantly with water depth, whereas OM nutritional quality was generally higher at shallower depths, with the unique exception at 600 m depth in 2010. Meiofaunal abundance and biomass (largely dominated by nematodes) showed the highest values at intermediate depths (ca 1500 m) in both sampling periods. The richness of meiofaunal higher taxa and nematode species richness did not vary significantly with water depth in both sampling periods. We suggest here that patterns in OM quantity, C degradation rates, and meiofauna community composition in 2011 were likely influenced by the intensification of the warm West Spitsbergen Current (WSC). We hypothesize that the intensity of the WSC inflow to the Arctic Ocean could have an important role on benthic biodiversity and functioning of deep-sea Arctic ecosystems.

## 1. Introduction

Deep-sea ecosystems can be highly complex, diverse and characterized by high spatial and temporal variability (Gage and Tyler, 1991; Danovaro et al., 2014 and citations therein), and increasingly subjected to multiple threats to which they are progressively and increasingly exposed (Ramirez-Llodra et al., 2011; Mengerink et al., 2014).

Continental margins, (extending from ca. 100–200 m to about 4000 m depth or more, Levin and Dayton, 2009) cover three million square kilometers, i.e. circa 20% of the world ocean surface (Walsh, 1991), and represent sites of intense exchange of energy and material between the continental shelves and the deep basins (Weaver et al., 2004). They play key roles in the global

biogeochemical cycles, are important reservoirs of organic C and can be hot spots of deep-sea biodiversity (Danovaro et al., 2009; Menot et al., 2010; Levin and Sibuet, 2012).

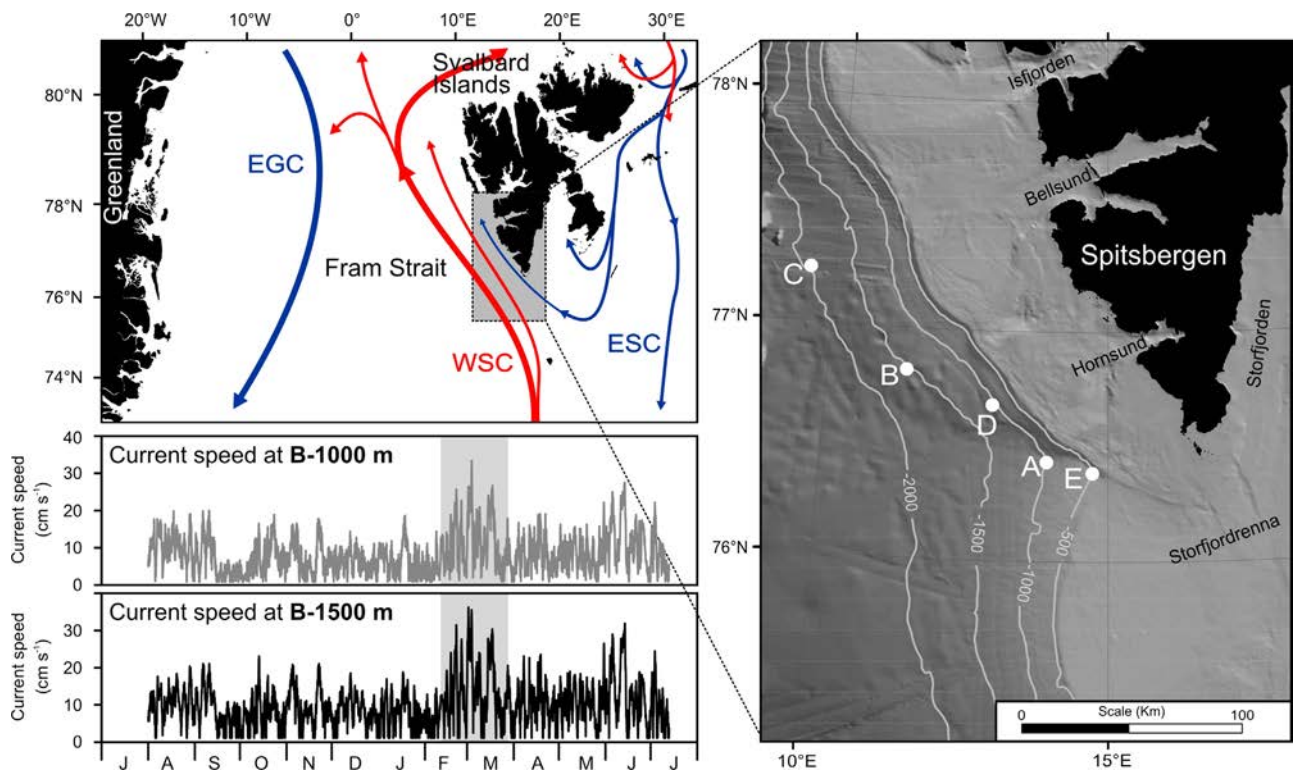
Ocean margin sediments (200–2000 m depth) can contribute about 30% of the mineralization in marine sediments (Middleburg et al., 1997). Biodiversity in soft bottoms is the key factor controlling the functioning of benthic ecosystems along the world's continental margins, so that the loss of even a few species might lead to the collapse of deep-sea ecosystems (Danovaro et al., 2008). Information on deep-sea benthic biodiversity along the Arctic margin is still relatively scarce (Włodarska-Kowalczyk et al., 2004; Renaud et al., 2006; Fonseca and Soltwedel, 2010; Fonseca et al., 2010), which makes it difficult to complete the complex mosaic of knowledge needed for assessing the effects of natural and anthropogenic constraints on these settings.

Moreover, although our knowledge of patterns of currents along continental margins is progressively increasing worldwide (including the Arctic; Hwang et al., 2015), information about the role of these currents on the structure and functioning of deep-sea

\* Corresponding author.

E-mail address: [apusceddu@unica.it](mailto:apusceddu@unica.it) (A. Pusceddu).

<sup>1</sup> Previous address: Dipartimento di Scienze della Vita e dell'Ambiente, Università Politecnica delle Marche, Ancona, Italia.



**Fig. 1.** Study area and sampling station locations. Red arrows show the warm Atlantic Water within the Western Spitsbergen Current (WSC), and blue arrows the cold East Greenland Current (EGC) and the Eastern Spitsbergen Current (ESC). Bathymetric data from IBCAO 3.0 (Jakobsson et al., 2012). Time series of current speeds measured at 1000 m and 1500 m depth at station B are also shown (see Sanchez-Vidal et al. (2015), for details on measurements). Shaded area shows the increase in the mean current speed in late winter 2011. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

benthic ecosystems in the Arctic is still limited (Glover et al., 2010). Therefore, considering also the importance of the C cycle at high latitudes (McGuire et al., 2009), there is a urgent need of investigating the potential role of currents on the biodiversity and ecosystem functions along the Arctic margin.

We analyzed contents, biochemical composition, nutritional quality and degradation rates of OM, meiofaunal abundance, biomass, and community composition, and nematode biodiversity in sediments collected (in July 2010 and July 2011) along a bathymetric transect (600–2000 m depth) located along the western margin of Spitsbergen (Svalbard Archipelago, Arctic Ocean) (Fig. 1). This is an area under the influence of the northward flowing West Spitsbergen Current (WSC), injecting warm Atlantic Water (AW) into the Arctic Ocean (Manley, 1995).

We focused our attention on meiofauna and nematodes as: (i) meiofauna (with abundances up to  $10^6$  individual per  $m^2$ ) are the most abundant metazoans in deep-sea sediments (Rex et al., 2006); (ii) nematodes are the dominant taxon of meiofauna (up to > 90% of total abundance; Lambshead, 2004); (iii) deep-sea meiofauna represents an important trophic link between organic detritus and higher trophic levels (Van Oevelen et al., 2011); and (iv) nematodes biodiversity is positively and exponentially linked with deep-sea ecosystem functioning (Danovaro et al., 2008). All these characteristics make meiofauna and nematodes ideal models to investigate the relationships between deep-sea benthic biodiversity and ecosystem functioning (Zeppilli et al., 2015, and citations therein).

## 2. Materials and methods

### 2.1. Study area

WSC represents the northernmost extension of the Norwegian

Atlantic Current (Aagaard et al., 1987). At about 79°N the WSC splits into two branches: one follows the perimeter of the Svalbard Islands and flows southwards forming the East Spitsbergen Current; the other one flows southwards along Greenland joining the East Greenland Current (EGC) in the western Fram Strait (Quadfasel et al., 1987). During its northward flow warm and saline AW loses heat due to surface heat exchange with the atmosphere, and freshens and cools as it mixes with ambient, less saline and cold waters (Saloranta and Haugan, 2004) with fjords contributions. In addition, in Storjorden, southeast of Spitsbergen, the prevailing easterly (offshore) winds over the island lead to a significant water cooling in the open part of the fjord and ice growth (Skogseth et al., 2005). This triggers an increase in the salinity and density of the ambient waters and convection, eventually reaching the bottom, thus leading to dense water formation that eventually overflows the outer fjord sill and cascades deep into the Fram Strait (Fer et al., 2003; Fer and Ådlandsvik, 2008). The transition zone between the North Atlantic and the Arctic Ocean in the western margin off Spitsbergen is the theatre for important heat and water exchanges. Here the northward transportation of warm and salty Atlantic Water at intermediate depths (~150–900 m) is believed to contribute in shaping the Arctic Ocean' ice cover (Polyakov et al., 2012), which, in turn, is expected to trigger a number of physical, chemical, and biological tipping points with potentially large impacts on the Arctic marine ecosystem (Duarte et al., 2012).

### 2.2. Sampling strategy

Sediment samples were collected during two cruises on board R/V Jan Mayen, in July 2010 and 2011 by means of a 50 cm × 50 cm × 50 cm box-corer at five stations, namely E, A, D, B and C, at 600, 1000, 1120, 1500 and 2000 m depth, respectively (Fig. 1 and Table 1).

Table 1

Year, water depth, latitude, longitude, sedimentary contents of organic matter (chlorophyll- $\alpha$ , phaeopigments, carbohydrates, proteins, lipids), meiofaunal abundance, biomass, and richness of taxa, and nematode biodiversity indices (SR=species richness; ES(51)=expected species number for 51 individuals; J=Pielou's index) in the sediments of the investigated stations. Latitude and longitude refers to the ship position.

Year	Depth (Station) (m)	Latitude (°N)	Longitude (°E)	Chlorophyll- $\alpha$ ( $\mu\text{g g}^{-1}$ )	Total phytopigment ( $\mu\text{g g}^{-1}$ )	Carbohydrates ( $\text{mg g}^{-1}$ )	Proteins ( $\text{mg g}^{-1}$ )	Lipids ( $\text{mg g}^{-1}$ )	Meiofaunal abundance (ind $10\text{ cm}^{-2}$ )	Meiofaunal biomass ( $\mu\text{g cm}^{-2}$ )	Richness of taxa	SR	ES(51)	J
2010	600 (E)	76°22.667'	14°35.723'	0.01 $\pm$ 0.01	0.23 $\pm$ 0.07	1.02 $\pm$ 0.18	1.26 $\pm$ 0.21	0.32 $\pm$ 0.05	673.2 $\pm$ 206.0	89.1 $\pm$ 41.7	11	68	30	0.88
2010	1000 (A)	76°26.545'	13°56.654'	0.34 $\pm$ 0.03	10.00 $\pm$ 0.73	1.49 $\pm$ 0.19	2.05 $\pm$ 0.16	0.52 $\pm$ 0.08	1303.0 $\pm$ 304.2	148.6 $\pm$ 112.5	9	69	29	0.86
2010	1120 (D)	76°40.981'	12°56.403'	0.35 $\pm$ 0.05	9.04 $\pm$ 1.05	1.14 $\pm$ 0.15	1.86 $\pm$ 0.37	0.31 $\pm$ 0.06	851.2 $\pm$ 214.4	130.4 $\pm$ 137.3	10	62	28	0.87
2010	1500 (B)	76°49.228'	11°25.126'	0.25 $\pm$ 0.07	8.79 $\pm$ 0.82	3.32 $\pm$ 0.50	3.92 $\pm$ 0.84	0.42 $\pm$ 0.03	1373.9 $\pm$ 208.5	146.4 $\pm$ 78.4	9	63	28	0.87
2010	2000 (C)	77°14.943'	09°32.460'	0.18 $\pm$ 0.00	6.78 $\pm$ 0.34	4.22 $\pm$ 1.33	2.59 $\pm$ 0.19	0.29 $\pm$ 0.01	727.4 $\pm$ 105.6	29.5 $\pm$ 13.5	8	62	28	0.88
2011	600 (E)	76°22.667'	14°35.723'	0.11 $\pm$ 0.01	5.76 $\pm$ 1.22	0.62 $\pm$ 0.11	0.41 $\pm$ 0.06	0.21 $\pm$ 0.05	561.8 $\pm$ 198.2	117.0 $\pm$ 124.0	10	75	33	0.92
2011	1000 (A)	76°26.545'	13°56.654'	0.19 $\pm$ 0.09	9.58 $\pm$ 1.01	4.27 $\pm$ 0.37	1.99 $\pm$ 0.45	0.53 $\pm$ 0.01	1062.3 $\pm$ 150.2	181.3 $\pm$ 70.0	10	63	26	0.83
2011	1120 (D)	76°40.981'	12°56.403'	0.08 $\pm$ 0.02	2.64 $\pm$ 0.04	0.95 $\pm$ 0.26	1.39 $\pm$ 0.33	0.26 $\pm$ 0.03	1036.5 $\pm$ 296.5	89.9 $\pm$ 22.1	12	59	26	0.86
2011	1500 (B)	76°49.228'	11°25.126'	0.08 $\pm$ 0.06	5.79 $\pm$ 0.14	4.06 $\pm$ 1.29	2.56 $\pm$ 0.52	0.47 $\pm$ 0.09	764.0 $\pm$ 142.0	93.4 $\pm$ 14.2	7	68	29	0.87
2011	2000 (C)	77°14.943'	09°32.460'	0.04 $\pm$ 0.01	4.85 $\pm$ 0.01	8.70 $\pm$ 0.30	1.84 $\pm$ 0.23	0.39 $\pm$ 0.05	749.0 $\pm$ 49.9	35.6 $\pm$ 4.8	7	62	26	0.83

In both sampling periods, meiofauna and OM analyses in each of the sampling sites were carried out on sediments obtained from triplicate Plexiglas corers (inner diameter 3.6 cm) obtained from: (i) two independent box-corer deployments in 2010 (with exception of the station at 600 m depth, where only one box-corer was successfully retrieved), and (ii) from one deployment per station in 2011, because of ship time restrictions.

For the OM, the first cm of each replicate sediment cores was stored at  $-20^\circ\text{C}$  until analysis. For the meiofauna, sediment cores were sliced each cm down to 10 cm and preserved at  $-20^\circ\text{C}$  until analysis.

In between the two cruises, four moorings were deployed at 1000 m (station A), 1120 m (station D), 1500 m (station B), and 2000 m (station C) depth (Fig. 1), equipped with one Technicap PPS3 sequential sampling sediment trap (12 collecting cups,  $0.125\text{ m}^2$  opening) at 25 m above the bottom (mab), and an Aanderaa current meter (RCM7/9). The sampling cups were filled up before deployment with a buffered 5% (v/v) formaldehyde solution in  $0.45\text{ }\mu\text{m}$  filtered seawater.

### 2.3. Sedimentary organic matter content, biochemical composition and degradation rates

Phytopigments were extracted using 3–5 mL 90% acetone (at  $4^\circ\text{C}$  in the dark for 12 h) from 0.5 g sediment samples. Chlorophyll- $\alpha$  and, after acidification of extracts with  $200\text{ }\mu\text{L}$  0.1 N HCl, phaeopigment contents were determined fluorometrically (Danovaro, 2010). Different methods for assessing chlorophyll- $\alpha$  concentrations in marine sediments can provide different under- or over-estimates (Pinckney et al., 1994) because of the relative importance of the chlorophylls' degradation products (Szymczak-Zyla and Kowalewska, 2007), which is a consistently observed feature in deep-sea sediments (Pusceddu et al., 2010). Therefore, for ease of consistency with previous investigations, we summed up chlorophyll- $\alpha$  and phaeopigment concentrations (i.e. total phytopigments), which were cumulatively used as a proxy of inputs of OM of algal origin (Pusceddu et al., 2010).

Protein, carbohydrate and lipid were determined spectrophotometrically, following the protocols detailed in Danovaro (2010), and their sedimentary contents ( $\text{mg g dry sediment}^{-1}$ ) expressed as bovine serum albumin, glucose and tripalmitine equivalents, respectively. Carbohydrate, protein and lipid sedimentary contents were converted into carbon equivalents using the conversion factors of 0.40, 0.49 and  $0.75\text{ }\mu\text{gC }\mu\text{g}^{-1}$ , respectively, and their sum defined as biopolymeric carbon (BPC; Fabiano et al., 1995).

For the purposes of the present study, the algal C contribution to the BPC, calculated as the percentage of phytopigment-to-BPC concentrations after converting the phytopigment concentrations into C equivalents using a mean value of  $40\text{ }\mu\text{gC }\mu\text{g}^{-1}$ , was used as a proxy of OM nutritional quality (Pusceddu et al., 2009).

OM degradation rates were estimated from aminopeptidase and beta-glucosidase activities determined by cleavage of fluorogenic substrates (L-leucine-4-methylcoumarinyl-7-amide, Leu-4-methylumbelliferone- $\beta$ -D-glucopyranoside, respectively) at saturating concentrations. 2.5 mL of sediment subsamples were incubated at *in situ* temperature in the dark for 2 h with 2.5 mL of filtered, sterile water containing  $200\text{ }\mu\text{M}$  L-leucine-4-methylcoumarinyl-7-amide and  $50\text{ }\mu\text{M}$  4-methylumbelliferol  $\beta$ -D-glucopyranoside, respectively, separately for aminopeptidase and  $\beta$ -glucosidase determinations. After incubation, the sediment slurries were centrifuged, and the supernatants analysed fluorometrically (Danovaro, 2010). The protease and glucosidase activities ( $\mu\text{mol substrate g}^{-1}\text{ h}^{-1}$ ) were converted into C degradation rates ( $\mu\text{gC g}^{-1}\text{ h}^{-1}$ ), using 72 as conversion factor (Pusceddu et al., 2014), and their sum referred to as C degradation rates. The turnover



( $d^{-1}$ ) of the biopolymeric C was calculated as the ratio of the hourly C degradation rate (once multiplied by 24) and the biopolymeric C content in the sediment.

#### 2.4. Total mass flux

Total mass flux data have been already reported elsewhere (Sanchez-Vidal et al., 2015). We have used those data to better substantiate our interpretation of the sedimentary data. Samples recovered from the sediment traps were stored in the dark at 2–4 °C until performing the subsequent analyses according to Heussner et al. (1990). Large swimming organisms were removed by wet sieving through a 1 mm nylon mesh, and organisms < 1 mm were hand-picked under a microscope with fine tweezers. Samples were split into 8 aliquots using a high precision peristaltic pump robot. The aliquots were repeatedly centrifuged to eliminate salt and formaldehyde, freeze-dried and weighed for total mass flux determination.

#### 2.5. Meiofaunal abundance and biomass

Each sample was treated with ultrasound (for 1 min 3 times, with 30 s intervals) to detach organisms from the grain particle surface and, then, sieved through a 1000- $\mu$ m and a 20- $\mu$ m mesh net to retain the smallest organisms. The fraction remaining on the latter sieve was re-suspended and centrifuged three times with Ludox HS40 diluted with water to a final density of 1.18 g cm $^{-3}$  (Heip et al., 1985). All specimens from 3 independent replicates per station were counted and sorted by taxa, under a stereomicroscope and after staining with Rose Bengal (0.5 g L $^{-1}$ ). Meiofaunal taxa representing < 1% of the total meiofaunal abundance were defined as rare taxa (Bianchelli et al. 2010). Meiofaunal biomass was assessed by bio-volumetric measurements of all retrieved specimens. Nematode biomass was calculated from their biovolume, using the Andrassy (1956) formula ( $V = L \times W^2 \times 0.063 \times 10^{-5}$ , in which body length,  $L$ , and width,  $W$ , are expressed in  $\mu$ m). Body volumes of all other taxa were derived from measurements of body length ( $L$ , in mm) and width ( $W$ , in mm), using the formula  $V = L \times W^2 \times C$ , where  $C$  is a dimensionless factor (specific for each meiofaunal taxon) used to convert  $L \times W^2$  to body volume, according to models relating body dimensions and volume (Feller and Warwick, 1988). Each body volume was multiplied by an average density of 1.13 g cm $^{-3}$  to obtain the biomass ( $\mu$ g DW:  $\mu$ g WW = 0.25; DW – dry weight and WW – wet weight, after Wieser, 1953) and the carbon content was considered to be 40% of the dry weight (Feller and Warwick, 1988).

#### 2.6. Nematode biodiversity

One-hundred specimens, or all of the retrieved nematodes if total nematode abundance was < 100, were randomly picked up from the first 2 cm of each of the independent replicates per station and sampling time, and were mounted on slides using the formalin–ethanol–glycerol technique (Seinhorst, 1959). Nematodes were identified to the species level or morphotypes (*sensu* De Mesel et al., 2006) according to Platt and Warwick (1983, 1988), Warwick et al. (1998) and the NeMys database (Vanaverbeke et al., 2015). Alpha diversity was calculated as species richness (SR) as the total number of species collected at each station, separately for the two sampling periods. Since species richness is strongly affected by the sample size, the expected species number [ES(X)] was calculated (Sanders, 1968, as modified by Hurlbert (1971)), to standardize the values of nematode diversity. The expected number of species for a theoretical sample of 51 specimens, ES(51), was selected (Gambi et al., 2014). Species evenness was measured using the Pielou's index (Pielou, 1975).

Beta diversity between the two sampling periods and among different depths within the same year was measured using similarity percentage (SIMPER) analyses and expressed as percentage of dissimilarity (Gray, 2000).

#### 2.7. Statistical analyses

Differences in each of the investigated variables (univariate tests) and their combinations (multivariate) among sampling depths ( $n=5$  fixed levels) were assessed, separately for the two sampling times, using permutational analyses of variance (PERMANOVA). The analyses were carried out on Euclidean distances (OM) or Bray–Curtis similarity matrices (faunal data) of previously normalized (OM) or untransformed (faunal) data, using 999 permutations of the residuals under a reduced model. For those PERMANOVA tests providing significant differences among sampling depths, pairwise tests were also carried out. Because of the restricted number of unique permutations,  $P$  values in the PERMANOVA and pairwise tests were obtained from Monte Carlo asymptotic distributions (Anderson and Robinson, 2003). Since PERMANOVA is sensitive to differences in multivariate dispersion among groups, we used also a test of homogeneity of dispersion (PERMDISP) to test the null hypothesis of equal dispersion among groups (Anderson et al., 2008). The results of these tests (data not shown) allowed confirming the null hypothesis for all multivariate tests (i.e., composition of OM, whole and rare meiofaunal taxa and nematode communities).

Canonical analysis of principal coordinates (CAP) was used in the multivariate contexts to ascertain the allocation of experimental groups to those established *a priori*. Results from the CAP were then used to visualize, using bi-plots, differences among experimental groups (i.e., among sampling depths). SIMPER analyses were performed to assess the percentage dissimilarity in the meiofaunal and nematode community composition among sampling depths separately for the two sampling times and for (i) the whole meiofaunal community, (ii) the meiofaunal rare taxa and (iii) the nematode assemblages. A ranked matrix of Bray–Curtis similarities, constructed on previously presence/absence transformed data, was used as input for the SIMPER tests.

To ascertain which among water depth, OM content (in terms of biopolymeric C) and nutritional quality (in terms of algal fraction of biopolymeric C) best explained meiofaunal abundance, biomass and community composition and nematode assemblage composition, distance-based linear models (DISTLM) analyses were carried out (McArdle and Anderson, 2001), based on Euclidean distance (meiofaunal abundance and biomass) and Bray–Curtis (meiofauna and nematode communities) similarity matrices.

The PERMANOVA, CAP, SIMPER and DISTLM analyses were performed using the routines included in the PRIMER 6+ software (Anderson et al., 2008).

### 3. Results

Data on the sedimentary contents of the organic compounds, along with the data of meiofaunal abundance, biomass, richness of taxa, and nematode biodiversity in the investigated stations and sampling periods are reported in Table 1.

#### 3.1. Sedimentary organic matter quantity, composition and degradation rates

Total phytopigment and biopolymeric C (BPC) sedimentary contents, OM composition and the algal fraction of BPC varied significantly with water depth in both sampling periods (Table 2).

**Table 2**

Output of the PERMANOVA analysis carried out to test for differences in total phytopigment and biopolymeric C contents, algal fraction of biopolymeric C (%) and organic matter (OM) composition, aminopeptidase,  $\beta$ -glucosidase and C degradation rates among sampling depths in July 2010 and July 2011 (DF=degrees of freedom; MS=mean square; Pseudo-F=F statistic; P(MC)=probability levels obtained from Monte Carlo asymptotic distributions); (\*\*\*)= $P < 0.001$ ; (\*\*)= $P < 0.01$ .

Variable	Source	July 2010				July 2011		
		df	MS	Pseudo-F	P(MC)	MS	Pseudo-F	P(MC)
<b>Total phytopigment</b>	Depth	4	3.411	96.292	0.001 (***)	3.215	28.143	0.001 (***)
	Residual	10	0.035			0.114		
<b>Biopolymeric C</b>	Depth	4	3.135	21.471	0.001 (***)	3.146	22.224	0.001 (***)
	Residual	10	0.146			0.142		
<b>OM composition</b>	Depth	4	15.456	18.909	0.001 (***)	15.318	17.552	0.001 (***)
	Residual	10	0.8174			0.8727		
<b>Algal fraction of BPC</b>	Depth	4	3.268	35.269	0.001 (***)	2.700	8.443	0.007 (**)
	Residual	10	0.093			0.320		
<b>Aminopeptidase</b>	Depth	4	3.254	33.001	0.001 (***)	2.687	8.268	0.004 (**)
	Residual	10	0.099			0.325		
<b><math>\beta</math>-glucosidase</b>	Depth	4	2.413	5.552	0.008 (**)	2.868	11.352	0.004 (**)
	Residual	10	0.435			0.253		
<b>C degradation</b>	Depth	4	3.236	30.620	0.001 (***)	2.675	8.099	0.007 (**)
	Residual	10	0.106			0.330		

In 2010 total phytopigment sedimentary contents at 600 m depth were significantly lower than those at all other sampling depths. In 2011 phytopigment contents did not show a clear pattern with depth (Table S1), though, notably, the lowest value was observed at 1120 m depth. BPC content varied significantly among depths in both sampling periods, with exceptions between 1500 m and 2000 m depth in both 2010 and 2011, between 600 m and 1120 m depth in 2010, and between 1000 m and 1500 m depth in 2011 (Table S1). Specifically, BPC content generally increased with increasing water depth from 600 m down to 1500 m depth in 2010, and down to 2000 m depth in 2011 (Fig. 2A).

The composition of sedimentary OM varied significantly among depths in both sampling periods (Table 2). Specifically, in 2010 differences among sampling depths were mostly driven by concentrations of all organic compounds which were consistently lower at 600 m depth than in all other sampling depths (Fig. 2B). In 2011, variations in the composition of OM among sampling depths were characterized by clear segregations of samples collected at shallow (600 m depth), intermediate (1000 m and 1120 m) and deeper (1500 m and 2000 m) depths (Table 2 and Fig. 2B).

In 2010, the value of the algal fraction of biopolymeric C at 600 m depth was significantly lower than in all other sampling depths, and highest values were observed at intermediate (1000–1120 m) water depths (Table S1 and Fig. 2C). The opposite was observed in 2011, when the highest algal fraction of biopolymeric C was found at 600 m depth, then decreased significantly with increasing water depth (Table S1).

Aminopeptidase,  $\beta$ -glucosidase and C degradation rates varied significantly among sampling depths in both years (Table 2). In 2010, aminopeptidase rates varied significantly among sampling depths, with exceptions between 600 and 1000 m, and between 1500 m and 1120 m and 2000 m depth. In 2011, significant differences were observed only between 600 m and 1000 m, 1500 m and 2000 m depth and between 1000 m and 1500 m, 2000 m depth (Table S1). These differences corresponded to a general increase in aminopeptidase rates with increasing water depth in

both sampling periods (Fig. 3A). In 2011,  $\beta$ -glucosidase rates were characterized by values at 1120 m depth which were higher than those at all other sampling depths in both years (Table S1 and Fig. 3B).

In 2010, C degradation rates at 1120 m and 2000 m depth were significantly higher than those at all other sampling depths, whereas in 2011 such rates increased significantly and progressively from 600 m to 1000 m to 1120–2000 m depth (Table S1 and Fig. 3C).

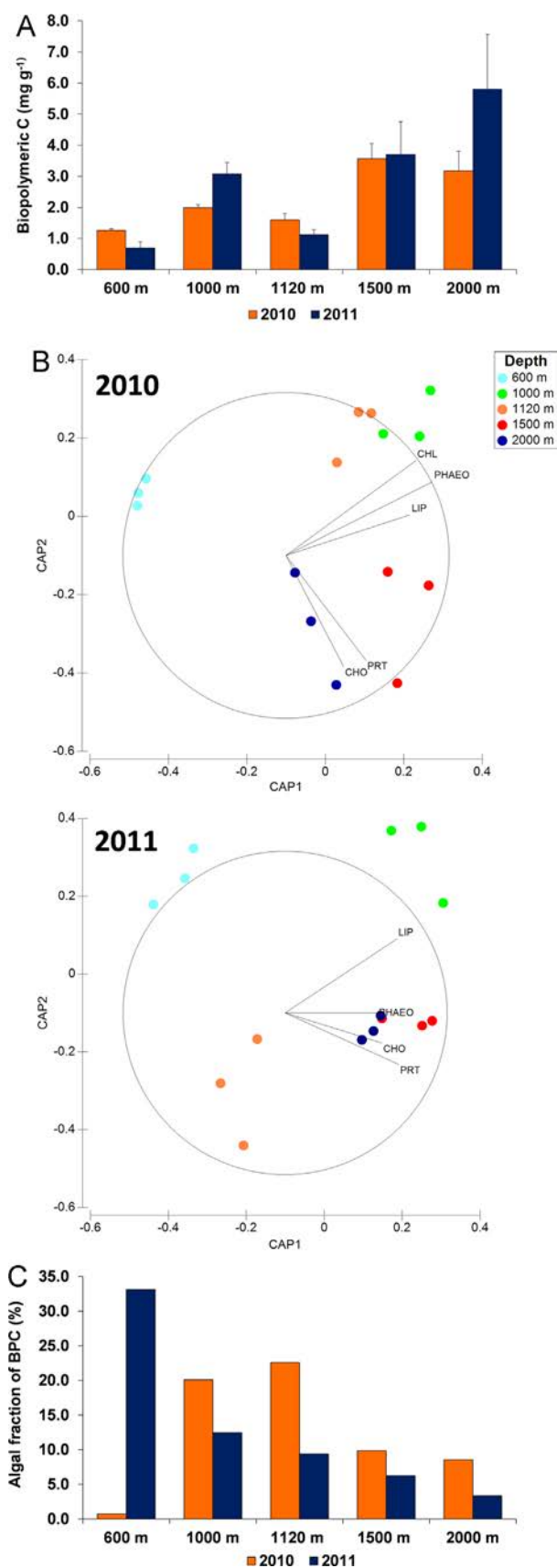
In both years, the potential daily turnover of biopolymeric C at 1120 m depth was higher than that in all other depths, with secondary maxima at the shallowest (600 m) and deepest (2000 m) sampling depths (Fig. 3D).

### 3.2. Total mass flux

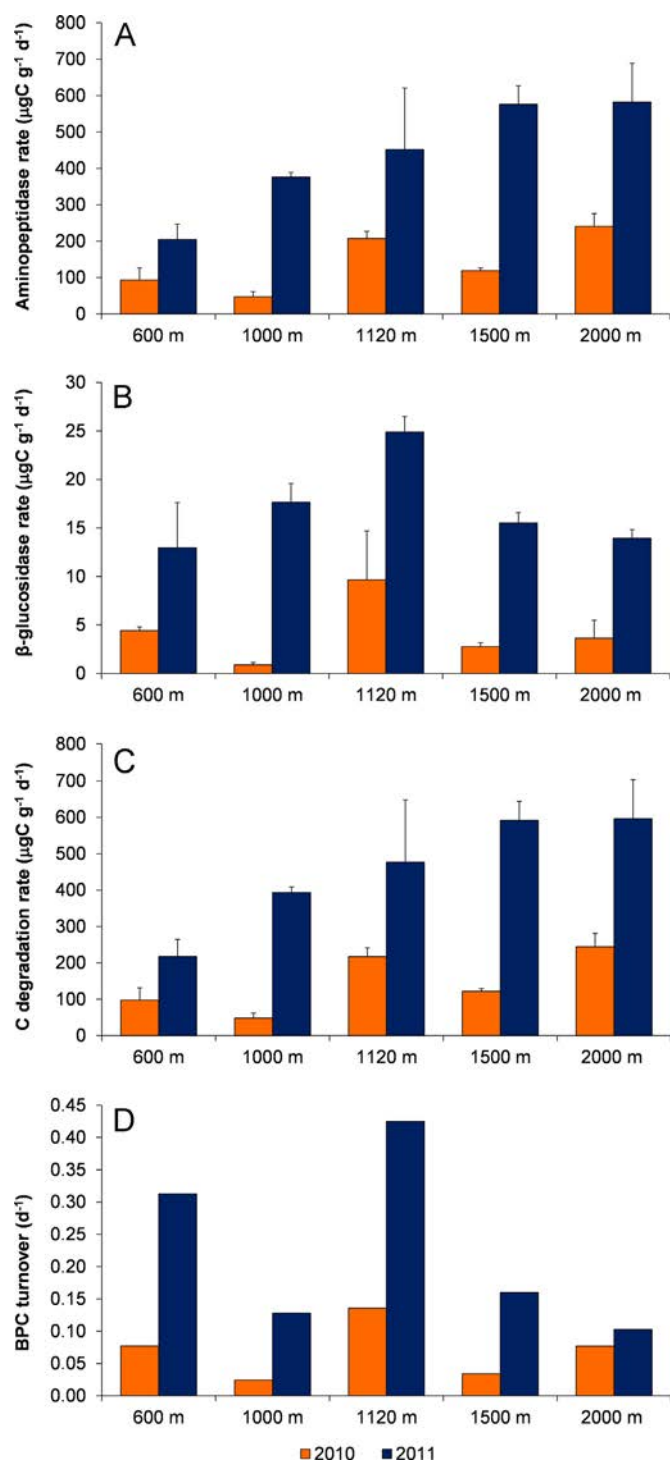
Temporal variations in total mass flux (TMF) at near bottom traps were characterized by high peaks in January, February and March 2011, especially at the shallowest and southernmost station A (maximum flux of  $11,646 \text{ mg m}^{-2} \text{ d}^{-1}$ ). TMF fluxes decreased northward and with time at all stations, though maintaining relatively high levels until the end of the study period (Fig. 4).

### 3.3. Total meiofaunal abundance, biomass and community structure

Total meiofaunal abundance varied significantly among depths in both sampling periods, whereas meiofaunal biomass and richness of taxa did not vary significantly (Table 3). The results of the pairwise tests reveal that in 2010 values of meiofaunal abundance at 1000 m and 1500 m depth were significantly higher than those at 600 and 2000 m depth, whereas in 2011 meiofaunal abundance at 1000 m depth was significantly higher than that at 600 m and 2000 m depth (Table S2). In both sampling periods and at all depths nematodes were the most abundant taxon (on average of the total meiofauna abundance, 96% in 2010 and 94% in 2011) followed by copepods (3% in 2010 and 5% in 2011) and polychaetes (0.5% in 2010 and 0.3% in 2011) (Fig. 5A). The rare taxa included



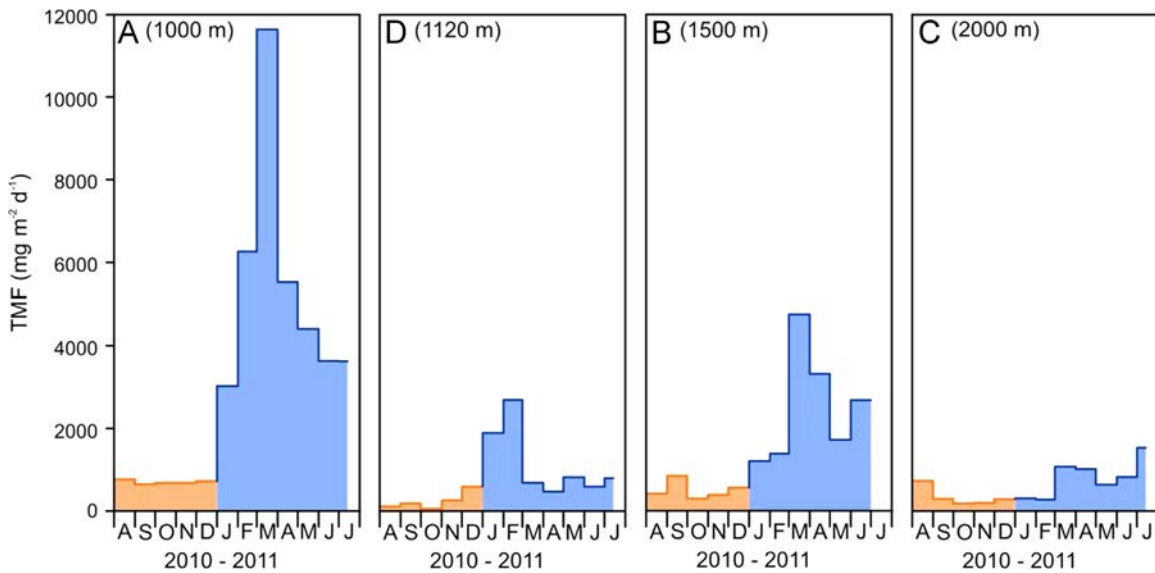
**Fig. 2.** Sedimentary organic matter in the top 1 cm of the sediment at each investigated depth in 2010 and 2011. (A) Concentration of biopolymeric C. (B) Variations in the biochemical composition of the sedimentary organic matter in July 2010 and 2011 (biplots obtained after canonical analysis of the principal coordinates; vectors are proportional to the Spearman correlation levels with  $r=0.5$  as a threshold; CHL for chlorophyll-a, PHAEO for phaeopigments, PRT for proteins, CHO for carbohydrates, LIP for lipids); (C) Percentage of algal fraction of biopolymeric C. Error bars denote standard deviations among replicates at each depth.



**Fig. 3.** Aminopeptidase (A),  $\beta$ -glucosidase (B) and C degradation rates in the sediments of the W Spitsbergen margin in July 2010 and 2011.

polychaetes, bivalves, ostracods, kinorhynch, oligochaetes, tardigrades, cumaceans, amphipods, isopods, acarins, priapulids, loriferans and cladocerans. Polychaetes and kinorhynch were encountered in both sampling periods at all depths. Amphipods and cladocerans occurred exclusively in 2010 samples, whereas loriferans were observed only in 2011 at all depths but 600 m depth.

In both sampling periods, the composition of the whole and rare meiofaunal communities varied significantly with water depth (Table 3).



**Fig. 4.** Time series of total mass flux (TMF,  $\text{mg m}^{-2} \text{d}^{-1}$ ) in the deep western Spitsbergen margin measured with near-bottom traps (25 mab) at 1000 m, 1120 m, 1500 m and 2000 m depth, from July 2010 (orange) to July 2011 (light blue). A, D, B and C within the frames correspond to stations in Fig. 1 ordered by increasing water depth. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

In both sampling periods significant differences in the composition of the whole meiofaunal communities were observed between 600 m and 1000 m depth, between 600 m and 1500 m depth, and between 1000 m and 2000 m depth. In 2010 significant differences were also observed between 1500 m and 1120 m and 2000 m depth. In 2011, significant differences were observed

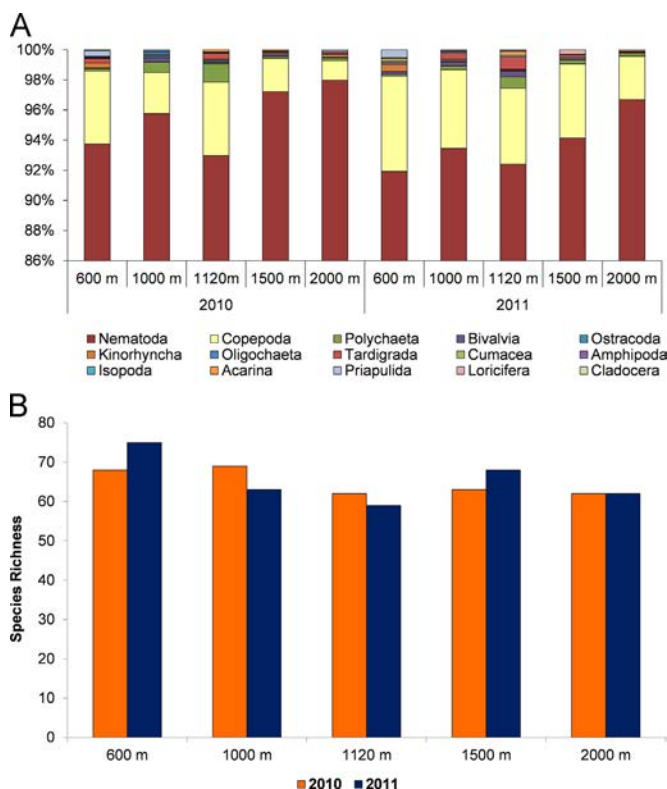
between 600 m and 2000 m, 1000 m and 2000 m, and 1120 m and 2000 m depth (Table S2).

Differences in the composition of rare meiofaunal community composition among sampling depths were less frequent than those observed for the whole communities. Specifically, in both sampling periods significant differences in the composition of rare

**Table 3**  
Output of the PERMANOVA analysis carried out to test differences in meiofaunal abundance, biomass, richness of taxa, and whole and rare community composition, nematode species richness, Pielou's J, expected species number (ES51), index of trophic diversity and community composition among sampling depths in July 2010 and July 2011 (DF=degrees of freedom; MS=mean square; Pseudo-F=F statistic; P(MC)=probability level after Monte Carlo tests); \*\*\*= $p < 0.001$ ; \*= $p < 0.05$ ; ns=not significant; na=not applicable.

Variable	Source	df	July 2010			July 2011		
			MS	Pseudo-F	P(MC)	MS	Pseudo-F	P(MC)
<b>Meiofaunal abundance</b>	Depth	4	325370.0	6.904	0.007 (**)	134480.0	3.899	0.004 (*)
	Residual	10	47126.0			34490.0		
<b>Meiofaunal biomass</b>	Depth	4	7602.9	0.959	0.475 (ns)	8351.7	1.987	0.169 (ns)
	Residual	10	7927.2			4203.2		
<b>Richness of meiofaunal taxa</b>	Depth	4	3.267	1.960	0.180 (ns)	7.7	1.933	0.200 (ns)
	Residual	10	1.667			4.0		
<b>Whole meiofauna community composition</b>	Depth	4	805.1	5.814	0.010 (**)	520.6	3.944	0.019 (*)
	Residual	10	138.5			132.0		
<b>Rare meiofauna community composition</b>	Depth	4	3226.8	3.510	0.002 (**)	2382.8	4.002	0.001 (***)
	Residual	10	919.2			595.5		
<b>Nematode species richness</b>	Depth	4	2.9	0.109	0.982 (ns)	51.1	1.707	0.244 (ns)
	Residual	10	27.0			29.9		
<b>Nematode Pielou's J</b>	Depth	4	0.001	0.368	0.822 (ns)	0.002	1.754	0.230 (ns)
	Residual	10	0.001			0.001		
<b>Nematode ES(51)</b>	Depth	4	0.76	0.154	0.959 (ns)	23.1	2.221	0.146 (ns)
	Residual	10	4.96			10.4		
<b>Nematode community composition</b>	Depth	4	4146.1	2.297	0.002 (**)	5455.4	3.609	0.001 (***)
	Residual	10	1805.1			1511.5		





**Fig. 5.** Community structure of the meiofaunal assemblage (A), and nematode species richness (B) at 600–2000 m depth in July 2010 and 2011. Species richness data illustrated in panel B are obtained by combining replicates.

meiofaunal taxa were observed between 1000 m and 600 m and 2000 m depth, and between 1120 m and 2000 m depth. In 2010 significant differences were observed also between 600 m and 1120 m, whereas in 2011 differences were significant between 1000 m and 1500 m (Table S2).

In both years whole meiofaunal beta diversity among sampling depths was relatively low, with values ranging from 25% (1120 m vs. 1500 m depth) to 34% (1000 m vs. 1120 m depth), and from 23% (600 m vs. 1120 m depth) to 38% (600 m vs. 2000 m depth), in 2010 and 2011, respectively. In 2010, the rare meiofaunal beta diversity among sampling depths was lowest (35% dissimilarity) between 1120 m and 1500 m depth and highest (47%) between 1120 m and 2000 m depth, whereas in 2011 it was lowest (30%) between 600 m and 1120 m depth and highest (52%) between 600 m and 2000 m depth.

### 3.4. Nematode biodiversity

Overall, 2839 nematode individuals were identified, belonging to 201 species, 92 genera and 25 families. Of the 201 nematode species encountered, 55 occurred only in 2010 and 43 were exclusively found in 2011. In both years the dominant family was Chromadoridae representing 22% in 2010 and 26% in 2011 of the total nematode abundance, followed by Desmoscolecidae (19%) in 2010 and Xyalidae (16%) in 2011. All the families were consistently found in both years, with exception of the family Coninckidae which was found only in 2010 at 1500 m (0.4%) and 2000 m (2.6%) depth.

In both sampling periods, none of the nematode diversity indices varied significantly among sampling depths (Fig. 5B and Table 3), whereas the composition of the nematode communities varied significantly among depths in both 2010 and 2011 (Table 3). In 2010 the composition of nematode communities varied

significantly only between 600 m and 2000 m depth (Table S2). Notably, in 2011 the nematode assemblage composition varied significantly between 600 m depth and all other sampling depths, with exception of 1120 m, between 1000 m and 1500–2000 m depth, and between 1120 m and 2000 m depth (Table S2).

In 2010 the nematode beta diversity among sampling depths was lowest (56%) between 1000 m and 1120 m depth and highest (69%) between 600 m and 2000 m depth. In 2011, the nematode beta diversity was lowest (55%) between 1500 m and 2000 m depth and highest (70%) between 1120 m and 2000 m depth.

### 3.5. Relationships between environmental variables and meiofaunal communities

The results of the DISTLM analysis carried out separately for the two sampling periods (Table S3) show that water depth, OM content and nutritional quality explain separately and cumulatively only very few proportions of meiofaunal abundance and biomass variance in both years. The few exceptions include: in 2010 a minor role of water depth on meiofaunal abundance and meiofaunal community composition (ca. 27% and 24% of explained variance, respectively) and in 2011 of OM nutritional quality on meiofaunal biomass and meiofaunal community composition (ca. 24% and 26%, respectively). In both sampling periods, variations in nematode assemblage composition were significantly explained by both water depth (ca. 16% and 22% of explained variance in 2010 and 2011, respectively) and OM nutritional quality (ca. 14% and 12% in 2010 and 2011, respectively).

## 4. Discussion

### 4.1. Sedimentary organic matter quantity, quality and turnover rates along the deep western Spitsbergen margin

Current meter data collected along the deep western Spitsbergen margin showed that cold DSWC did not occur between July 2010 and July 2011 (Sanchez-Vidal et al., 2015), but revealed the occurrence of an increased along slope poleward flow of the WSC (Fig. 1), with remote influence of the shallower, warmer, and saltier Atlantic Water (Sanchez-Vidal et al., 2015). Indeed, increased warm Atlantic Water transport in the core of the WSC in 2011 may have caused a shift in zooplankton community composition towards Atlantic species (Kraft et al., 2013). Higher near bottom currents speeds, according to the data obtained from trap-measured downward particle fluxes, likely caused a resuspension of fine sediments in the upper slope, transported and deposited them northward, and, according to previous findings (Lalande et al., 2011), determined significant changes in the composition of fluxes in the Fram Strait (Sanchez-Vidal et al., 2015). The increase in current speed reported during spring 2011 appears to be consistently observed at depths ranging from 750 to 1500 m depth at Station B (Fig. 1; data reported in Sanchez-Vidal et al. (2015)). This would suggest that current speed could have increased also at higher depths (i.e. down to 2000 m depth). Nevertheless, we report here that OM contents in the sediment of the Fram Strait increased significantly with water depth and that OM contents at 2000 m depth were significantly higher than those at all other depths in both years. Previous studies conducted in a number of continental margins along different European Seas showed that increasing sedimentary contents of biopolymeric C with increasing water depth, though rarely observed (Pusceddu et al., 2010; Duros et al., 2011), can occur as a result of either recurrent or episodic events of water masses transported downward (Heussner et al., 2006), eventually canalized by submarine canyons (Canals et al., 2006; de Stigter et al., 2007; Tyler et al., 2009; Pusceddu et al.,

2013). Our results show that, in 2011, the biopolymeric C sedimentary content at 2000 m depth along the deep western Spitsbergen margin was 2- to 8-times higher than that at the other sampling depths, revealing a general increase with increasing water depth. This figure is therefore consistent with the occurrence of active resuspension and transport of surface sediments from the upper slope to the deep basin, at least down to 1000 m depth (Fig. 4), likely mediated by the intensification of the WSC, either in February–March 2011 or June–July 2011 (Fig. 1).

We report here also that in 2011 the algal fraction of biopolymeric C, utilised as a proxy of the freshness, and, thus, nutritional quality of organic C, decreased with increasing water depth. This result is consistent with the results obtained from other European continental margins (Pusceddu et al., 2010), and suggests that the deeper part of the deep western Spitsbergen margin, particularly in 2011, was characterised by an accumulation of large amounts of OM of low nutritional value. This hypothesis is also confirmed by the OC turnover rates, which were lowest in the deepest portion of the investigated margin and, at the same time, were coupled with the highest rates of potential degradation of OC (Fig. 3). These results suggest that the OC deposited at 2000 m in 2011 were characterised by a pre-eminent refractory nature that, on the one hand, stimulated higher degradation activities, but, on the other one, led to OC turnover times lower than those observed at shallower depths.

Altogether these results suggest that in 2011 the WSC intensification over the slope off Storfjorden was a major factor modulating the input, bioavailability and turnover time of OM deposited on the seafloor of the investigated area. Our results show that OM sedimentary contents increased with increasing water depth also in 2010 (though with an apparently smoother trend than that observed in 2011), leading us to hypothesize that the increased transport by the WSC possibly occurred in 2010 also. However, the absence of current data prior to July 2010 recommend considering the hypothesis of WSC intensification in 2010 with caution. While further *in situ* studies are required to fully confirm that this “warming” phenomenon is a recurrent one along the Spitsbergen margin, this would imply that the role of the deepening warm branch of WSC on the OM contents in the deep-sea basin along the western Svalbard margin could mirror that of “cooling” DSWC events observed along some submarine canyons in the Mediterranean Sea (Pusceddu et al., 2013). The observation that in 2010 the nutritional quality of OM (i.e. the algal fraction of BPC) was lowest at the shallower depth, peaked up at intermediate depths (1000–1120 m depth) and decreased again down to 2000 m depth, suggests that other factors (not investigated here) could have influenced the distribution and nutritional quality of OM in 2010. For instance, we cannot exclude that the bathymetric distribution of OM contents and nutritional quality in the deepest part of the western Spitsbergen margin could have been determined (in both years) also by concurrent mechanisms of particle horizontal redistribution or lateral advection mediated by bottom currents acting at local spatial scales (not addressed in this study), as recently reported for the Whittard Canyon in the NE Atlantic (Amaro et al., 2015).

#### 4.2. Meiofaunal abundance, biomass and biodiversity along the deep western Spitsbergen margin

Both in 2010 and 2011, the lowest values of meiofaunal abundance were observed at 600 and 2000 m depth, whereas the highest values occurred at intermediate depths (i.e., 1000–1500 m depth). Such hump-shaped distribution in meiofaunal abundance along the deep western Spitsbergen margin, in contrast with previous studies carried out worldwide reporting a general decrease of values with increasing water depth (Soltwedel, 2000),

has emerged recently as a feature of highly dynamic continental margins, at times indented by submarine canyons (Bianchelli et al., 2010). In this regard, the lack of an expected decrease of meiofaunal abundance and the overall invariance of meiofaunal biomass with increasing water depth allows us hypothesizing that the deep western Spitsbergen margin is exposed to such hydrodynamic conditions able not only to modify the quantity and availability of resources for the benthos, but also to influence the abundance and biomass of the most abundant heterotrophic metazoans (i.e. meiofauna). Moreover, at least in 2011, the hump-shaped curve in the distribution of meiofaunal abundance could be partially the result of (i) the effect of WSC in the upper part of the slope, likely causing the resuspension of meiofauna at 600 m depth, and (ii) the decreased OM availability at 2000 m depth. This suggests WSC flow exerting, through sediment resuspension, a direct physical stress on meiofauna in the upper slope and an indirect effect in the deeper slope by injecting low-quality food particles diluted in a mostly inorganic or refractory bulk mass flux. The hypothesis of an effect of sediment resuspension at 600 m depth could be partially corroborated by the presence, in 2011, of meiofauna with average individual biomass higher - and thus putatively less susceptible to resuspension - than in any other sampling depth (Fig. 6). A similar situation, possibly driven by the more pronounced impacts of sediment resuspension on smaller individuals, has been also observed in deep-sea regions impacted by bottom trawling, where large individuals appear less affected by the impacts of sediment resuspension (Pusceddu et al., 2014). This, however, apparently does not hold true in 2010, when the individual body size of meiofauna was more variable and characterised by an unclear pattern with increasing water depth. Moreover, we show here that in both years the variability in the individual biomass of meiofauna at each depth is very high, with exception at 2000 m depth, and generally larger than the variability among depths (Fig. 6). This indicates that the effects of sediment resuspension possibly associated with the intensification of WSC flow on the individual biomass of meiofauna in the upper margin are not significant and, if any, are much less relevant than those caused by bottom trawling. In both sampling periods, number of meiofaunal higher taxa and nematode species richness did not vary among sampling depths, confirming patterns observed in different continental margins both in the Atlantic and Mediterranean Sea (Danovaro et al., 2009; Bianchelli et al., 2010). Nevertheless, some depth-related variations in the composition of the whole and rare meiofaunal communities and nematode assemblages occurred in both 2010 and 2011. In 2010, differences in the composition of meiofaunal communities and nematode assemblages were confined to the upper part of the margin, whereas

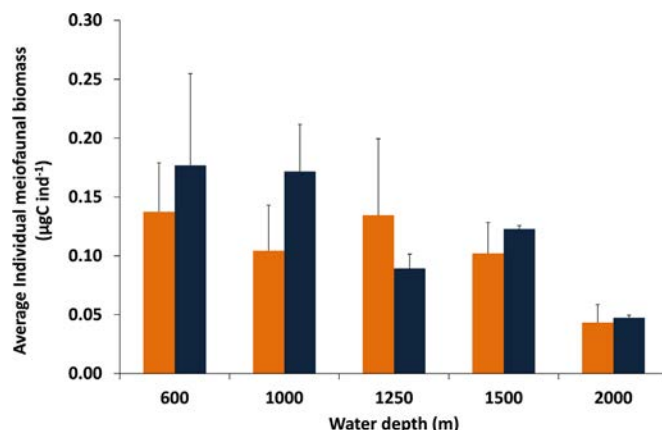


Fig. 6. Meiofaunal individual biomass at each investigated depth in the two sampling years.

differences in 2011 were more pronounced and evident also at larger depths (Table S2). The different turnover diversity across sampling depths in the two years is difficult to explain, but it could be possibly due to the pseudo-replication that affected sampling in some stations, due to technical constraints.

It is worth noting that recent studies conducted along other continental margins characterised by a strong hydrodynamism have highlighted the co-occurrence of a general invariance in the number of meiofaunal taxa or nematode genus/species, accompanied by a large turnover diversity across stations located at different water depths (e.g. Ingels et al. (2011) and Danovaro et al. (2013)). Moreover, although nematodes were, in both years and at all depths, the dominant component, we report here that in 2011, the relative importance of harpacticoid (endo-benthic) copepods at the station putatively most impacted by the intensification of bottom currents (600 m depth; 6.3% of the total meiofaunal abundance) was higher than that observed in deeper settings (down to 2.9% at 2000 m depth). Since these copepods have a life style similar to that of nematodes but a larger individual body size (on average  $0.42 \mu\text{gC ind}^{-1}$  vs.  $0.08 \mu\text{gC ind}^{-1}$  of nematodes), this finding further supports the hypothesis that sediment resuspension induced by WSC could influence the deep western Spitsbergen margin benthic ecosystems.

#### 4.3. Relationships between food availability and meiofauna biodiversity

We report here that the three variables commonly hypothesised to represent the most important factors affecting meiofaunal features in deep-sea sediments (namely water depth, OM content and nutritional quality; Gambi et al., 2014) had only minor and inter-annually variable effects on meiofaunal abundance, biomass and community composition.

The almost idiosyncratic relationship between meiofaunal standing stocks and OM quantity and nutritional quality observed in this study is in contrast with what generally observed along other continental margins at similar depths (Bianchelli et al., 2010) and is difficult to explain. This counterintuitive pattern could be the result of either the minimal temporal replication of our study or the potentially disrupting effects of sediment resuspension induced by the intensification of WSC on meiofauna distribution.

The results of the DISTLM analysis show also that both water depth and OM nutritional quality explained significant and relatively high proportions of nematode community composition variability. The key role of water depth and OM quality in explaining patterns in nematode community composition in this study confirms previous findings obtained along other continental margins (Danovaro et al., 2009). These results suggest that, in the deep sea, nematode assemblages are affected by sedimentary OM nutritional quality more than meiofauna communities as a whole.

## 5. Conclusions

Our sampling strategy was partially affected by under-replication at both spatial and temporal scales. Moreover, we cannot ascertain whether intensified WSC events are a recurrent natural or episodic event (Beszczynska-Möller et al., 2012). However, data presented here let us to hypothesize that an intensification of the warm WSC along the deep western Spitsbergen slope in winter-spring 2011 could have influenced both OC supply (Sanchez-Vidal et al., 2015), C accumulation, the nutritional quality and the turnover of organic matter in the sediments. Such features were associated with changes in meiofaunal community structure down to the deepest portion of the western Spitsbergen margin. Since the Arctic is impacted by climate change to a higher extent than

any other world ocean (Wadhams and Davis, 2000; Wadhams, 2012), we stress here the need of further studies addressing scales of temporal variability of the structure and function of the deep Arctic margin ecosystems.

## Acknowledgments

This study has been conducted in the framework of the Project HERMIONE funded by the European Commission under the Framework Program VII (Contract FP7-ENV-2008-1-226354). MC and ASV also acknowledge the support provided by the GRACCIE-CONSOLIDER (CSD2007-00067) project, and a Catalan Government Grups de Recerca Consolidats grant (2014 SGR 1068). The authors are indebted with Stephan Buenz, researchers and the crew on board R/V “Jan Mayen” (University of Tromsø, Norway) for their help during the cruises.

## Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.dsr.2015.11.004>.

## References

- Aagaard, K., Foldvik, A., Hillman, S.R., 1987. The West Spitsbergen Current: disposition and water mass transformation. *J. Geophys. Res.* 92, 3778–3784.
- Amaro, T., de Stigter, H., Lavaleye, M., Duineveld, G., 2015. Organic matter enrichment in the Whittard Channel (northern Bay of Biscay margin, NE Atlantic); its origin and possible effects on benthic megafauna. *Deep Sea Res. I* 102, 90–100.
- Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. PRIMER-E, Plymouth, UK.
- Anderson, M.J., Robinson, J., 2003. Generalised discriminant analysis based on distances. *Aust. N. Z. J. Stat.* 45, 301–318.
- Andrassy, I., 1956. The determination of volume and weight of nematodes. *Acta Zool.* 2, 1–15.
- Beszczynska-Möller, A., Fahrbach, E., Schauer, U., Hansen, E., 2012. Variability in Atlantic water temperature and transport at the entrance to the Arctic Ocean, 1997–2010. *ICES J. Mar. Sci.* 69, 852–863.
- Bianchelli, S., Gambi, C., Zeppilli, D., Danovaro, R., 2010. Metazoan meiofauna in deep-sea canyons and adjacent open slopes: a large-scale comparison with focus on the rare taxa. *Deep Sea Res. I* 57, 420–433.
- Canals, M., Puig, P., Durrieu de Madron, X., Heussner, S., Palanques, A., Fabres, J., 2006. Flushing submarine canyons. *Nature* 444, 354–357.
- Danovaro, R., 2010. Methods for the Study of Deep-Sea Sediments, Their Functioning and Biodiversity. CRC Press Taylor & Francis Group, Boca Raton, FL, USA, p. 428.
- Danovaro, R., Canals, M., Gambi, C., Heussner, S., Lampadariou, N., Vanreusel, A., 2009. Exploring patterns and hot spots of benthic biodiversity on the slopes of European margins. *Oceanography* 22 (1), 16–26.
- Danovaro, R., Carugati, L., Corinaldesi, C., Gambi, C., Guilini, K., Pusceddu, A., Vanreusel, A., 2013. Multiple spatial scale analyses provide new clues on patterns and drivers of deep-sea nematode diversity. *Deep-Sea Res. II* 92, 97–106.
- Danovaro, R., Gambi, C., Dell’Anno, A., Corinaldesi, C., Franchetti, S., Vanreusel, A., Vincx, M., Gooday, A.J., 2008. Exponential decline of deep-sea ecosystem functioning linked to benthic biodiversity loss. *Curr. Biol.* 18, 1–8.
- Danovaro, R., Snelgrove, P.V.R., Tyler, P., 2014. Challenging the paradigms of deep-sea ecology. *Trends Ecol. Evol.* 29, 465–475.
- De Mesel, I., Lee, H.J., Vanhove, S., Vincx, M., Vanreusel, A., 2006. Species diversity and distribution within the deep-sea nematode genus *Acantholaimus* on the continental shelf and slope in Antarctica. *Polar Biol.* 29, 860–871.
- de Stigter, H., Boer, W., de Jesús Mendes, P.A., Jesús, C.C., Thomsen, L., van den Berg, G.D., van Weering, T.C.E., 2007. Recent sediment transport and deposition in Nazaré Canyon, Portuguese continental margin. *Mar. Geol.* 246, 144–164.
- Duarte, C.M., Agusti, S., Wassmann, P., Arrieta, J.M., Alcaraz, M., Coello, A., Marba, N., Hendriks, I.E., Holding, J., Garcia-Zarandona, I., Kritzbeg, E., Vague, D., 2012. Tipping elements in the Arctic Marine Ecosystem. *Ambio* 4, 44–55.
- Duros, P., Fontanier, C., Metzger, E., Pusceddu, A., Cesbron, F., deStigter, H.C., Bianchelli, S., Danovaro, R., Jorissen, F.J., 2011. Live (stained) benthic foraminifera in the Whittard Canyon, Celtic margin (NE Atlantic). *Deep Sea Res. I* 58, 128–146.
- Fabiano, M., Danovaro, R., Franchetti, S., 1995. A three-year time series of elemental and biochemical composition of organic matter in subtidal sandy sediments of the Ligurian Sea (north western Mediterranean). *Cont. Shelf Res.* 15, 1453–1469.
- Feller, R.J., Warwick, R.M., 1988. Energetics. In: Higgins, R.P., Thiel, H. (Eds.), *Introduction to the Study of Meiofauna*. Smithsonian Institution Press, London, pp. 181–196.



- Fer, I., Ådlandsvik, B., 2008. Descent and mixing of the overflow plume from Storfjorden Svalbard: an idealized numerical model study. *Ocean Sci.* 4, 115–132.
- Fer, I., Skogseth, R., Haugan, P.M., Jaccard, P., 2003. Observations of the Storfjorden overflow. *Deep-Sea Res.* 50, 1283–1303.
- Fonseca, G., Soltwedel, T., 2010. Deep-sea meiobenthic communities underneath the marginal ice zone off Eastern Greenland. *Polar Biol.* 30, 607–618.
- Fonseca, G., Soltwedel, T., Vanreusel, A., Lindegarth, M., 2010. Variation in nematode assemblages over multiple spatial scales and environmental conditions in Arctic deep seas. *Prog. Oceanogr.* 84, 174–184.
- Gage, J.D., Tyler, P.A., 1991. *Deep-sea Biology: a Natural History of Organisms at the Deep-sea Floor*. Cambridge University Press, Cambridge, Great Britain, p. 504.
- Gambi, C., Pusceddu, A., Benedetti-Cecchi, L., Danovaro, R., 2014. Species richness, species turnover, and functional diversity in nematodes of the deep Mediterranean Sea: searching for drivers at different spatial scales. *Glob. Ecol. Biogeogr.* 23, 24–39.
- Glover, A.G., Gooday, A.J., Bailey, D.M., Billett, D.S.M., Chevaldonne, P., Colaco, A., Copley, J., Cuvellier, D., Desbruyères, D., Kalogeropoulos, V., Klages, M., Lampadarios, N., Lejeune, C., Mestre, N.C., Paterson, G.L.J., Perez, T., Ruhl, H., Sarrazin, J., Soltwedel, T., Soto, E.H., Thatje, S., Tselepidis, A., Van Gaever, S., Vanreusel, A., 2010. Temporal change in deep-sea Benthic Ecosystems: a review of the evidence from recent time-series studies. *Adv. Mar. Biol.* 58, 1–95.
- Gray, J.S., 2000. The measurement of marine species diversity, with an application to the benthic fauna of the Norwegian continental shelf. *J. Exp. Mar. Biol. Ecol.* 250, 23–49.
- Heip, C., Vincx, M., Vranken, G., 1985. The ecology of marine nematodes. *Oceanogr. Mar. Biol. Annu. Rev.* 23, 399–489.
- Heussner, S., Ratti, C., Carbonne, J., 1990. The PPS 3 timeseries sediment trap and the trap sample techniques used during the ECOMARGE experiment. *Cont. Shelf Res.* 10, 943–958.
- Heussner, S., Durrieu de Madron, X., Calafat, A., Canals, M., Carbonne, J., Delsaut, N., Saragoni, G., 2006. Spatial and temporal variability of downward particle fluxes on a continental slope: lessons from an 8-yr experiment in the Gulf of Lions (NW Mediterranean). *Mar. Geol.* 234, 63–92.
- Hurlbert, S.H., 1971. The non-concept of species diversity: a critique and alternative parameters. *Ecology* 52, 577–586.
- Hwang, J., Kim, M., Manganini, S.J., McIntyre, C.P., Haghipour, N., Park, J.J., Krishfield, R.A., Macdonald, R.W., McLaughlin, F.A., Eglinton, T.I., 2015. Temporal and spatial variability of particle transport in the deep Arctic Canada Basin. *J. Geophys. Res. Oceans* 120, 2784–2799.
- Ingels, J., Tchesunov, A.V., Vanreusel, A., 2011. Meiofauna in the Gollum Channels and the Whittard Canyon, Celtic Margin—how local environmental conditions shape nematode structure and function. *PLoS One* 6 (5), e20094.
- Jakobsson, M., Mayer, L., Coakley, B., Dowdeswell, J.A., Forbes, S., Fridman, B., Hodnesdal, H., Noormets, R., Pedersen, R., Rebesco, M., Schenke, H.W., Zarayskaya, Y., Accettella, D., Armstrong, A., Anderson, R.M., Bienhoff, P., Cammerlinghi, A., Church, I., Edwards, M., Gardner, J.V., Hall, J.K., Hell, B., Hestvik, O., Kristoffersen, Y., Marcussen, C., Mohammad, R., Mosher, D., Nghiem, S.V., Pedrosa, M.T., Travaglini, P.G., Weatherall, P., 2012. The international bathymetric chart of the arctic ocean (IBCAO) version 3.0. *Geophys. Res. Lett.* 39, L12609.
- Kraft, A., Nöthig, E.M., Bauerfeind, E., Wildish, D.J., Pohle, G.W., Bathmann, U.V., Beszczynska-Möller, A., Klages, M., 2013. First evidence of reproductive success in a southern invader indicates possible community shifts among Arctic zooplankton. *Mar. Ecol. Prog. Ser.* 493, 291–296.
- Lalande, C., Bauerfeind, E., Nöthig, E.M., 2011. Downward particulate organic carbon export at high temporal resolution in the eastern Fram Strait: influence of Atlantic waters on flux composition. *Mar. Ecol. Prog. Ser.* 440, 127–136.
- Lambhead, P.J.D., 2004. Marine nematode biodiversity. In: Chen, Z.X., Chen, S.Y., Dickson, D.W. (Eds.), *Nematology: Advances and Perspectives. Vol 1: Nematode Morphology, Physiology and Ecology*. CABI Publishing, Wallingford, U.K., pp. 436–467.
- Levin, L.A., Dayton, P.K., 2009. Ecological theory and continental margins: where shallow meets deep. *Trends Ecol. Evol.* 24, 606–617.
- Levin, L.A., Sibuet, M., 2012. Understanding continental margin biodiversity: a new imperative. *Annu. Rev. Mar. Sci.* 4, 49–112.
- Manley, T.O., 1995. Branching of Atlantic water within the Greenland-Spitsbergen passage: an estimate of recirculation. *J. Geophys. Res.* 100, 20627–20634.
- McArdle, B.H., Anderson, M.J., 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology* 82, 290–297.
- McGuire, A.D., Anderson, L.G., Dallimore, S., Guo, L., Hayes, D.J., Heimann, M., Loreson, T.D., MacDonald, R.W., Roulet, N., 2009. Sensitivity of the carbon cycle in the Arctic to climate change. *Ecol. Monogr.* 79, 523–555.
- Mengerink, K.J., Van Dover, C.L., Ardrin, J., Baker, M., Escobar-Briones, E., Gjerde, K., Koslow, J.A., Ramirez-Llodra, E., Lara-Lopez, A., Squires, D., Sutton, T., Sweetman, A.K., Levin, L.A., 2014. A call for deep-ocean stewardship. *Science* 344, 696–698.
- Menot, L., Sibuet, M., Carney, R.S., Levin, L.A., Rowe, G.T., Billett, D., Poore, G.C.B., Kitazato, H., Vanreusel, A., Galéron, J., Lavrado, H.P., Sellanes, J., Ingole, B., Krylova, E.M., 2010. New perceptions of continental margin biodiversity. In: McIntyre, A.D. (Ed.), *Life in the World's Oceans: Diversity, Distribution and Abundance*. John Wiley & Sons, Chichester, United Kingdom, pp. 79–102.
- Middleburg, J.J., Soetaert, K., Herman, P.M.J., 1997. Empirical relationships for use in global diagenetic models. *Deep-Sea Res.* 44, 327–344.
- Pielou, E.C., 1975. *Ecological Diversity*. John Wiley & Sons, New York.
- Pinckney, J., Papa, R., Zingmark, R., 1994. Comparison of high-performance liquid chromatographic, spectrophotometric and fluorometric methods for determining chlorophyll a concentrations in estuarine sediments. *J. Microbiol. Methods* 19, 59–66.
- Platt, H.M., Warwick, R.M., 1983. *Free Living Marine Nematodes. Part I. British Enoplids*. Cambridge University Press, Cambridge.
- Platt, H.M., Warwick, R.M., 1988. *A Synopsis of the Free Living Marine Nematodes. Part II: British Chromadorids*. Cambridge University Press, Cambridge.
- Polyakov, I.V., Walsh, J.E., Kwok, R., 2012. Recent changes of arctic multiyear sea ice coverage and the likely causes. *Bull. Am. Meteorol. Soc.* 93, 145–151.
- Pusceddu, A., Bianchelli, S., Canals, M., Durrieu de Madron, X., Heussner, S., Lykousis, V., de Stigter, H., Danovaro, R., 2010. Organic matter in sediments of canyons and open slopes along European continental margins. *Deep-Sea Res.* 57, 441–457.
- Pusceddu, A., Bianchelli, S., Martín, J., Puig, P., Palanques, A., Masqué, P., Danovaro, R., 2014. Chronic and intensive bottom trawling impairs deep-sea biodiversity and ecosystem functioning. *Proc. Natl. Acad. Sci. USA* 111 (24), 8861–8866.
- Pusceddu, A., Dell'Anno, A., Fabiano, M., Danovaro, R., 2009. Quantity and bioavailability of sediment organic matter as signatures of benthic trophic status. *Mar. Ecol. Prog. Ser.* 375, 41–52.
- Pusceddu, A., Mea, M., Canals, M., Heussner, S., Durrieu de Madron, X., Sanchez-Vidal, A., Bianchelli, S., Corinaldesi, C., Dell'Anno, A., Thomsen, L., Danovaro, R., 2013. Major consequences of an intense dense shelf water cascading event on deep-sea benthic trophic conditions and meiofaunal biodiversity. *Biogeosciences* 10, 2659–2670.
- Quadfasel, D., Gascard, J.C., Koltermann, K.P., 1987. Large-scale oceanography in Fram Strait during the 1984 Marginal Ice Zone experiment. *J. Geophys. Res.* 92, 6719–6728.
- Ramirez-Llodra, E.Z., Tyler, P.A., Baker, M.C., Bergstad, O.A., Clark, M.R., Escobar, E., Levin, L.A., Menot, L., Rowden, A.A., Smith, C.R., Van Dover, C.L., 2011. Man and the last great wilderness: human impact on the deep sea. *PLoS One* 6 (8), e22588.
- Renaud, P.E., Ambrose Jr., W.G., Vanreusel, A., Clough, L.M., 2006. Nematode and macrofaunal diversity in central Arctic Ocean benthos. *J. Exp. Mar. Biol. Ecol.* 330, 297–306.
- Rex, M.A., Etter, R.J., Morris, J.S., Crouse, J., McClain, C.R., Johnson, N.A., Stuart, C.T., Deming, J.W., Thies, R., Avery, R., 2006. Global bathymetric patterns of standing stock and body size in the deep-sea benthos. *Mar. Ecol. Prog. Ser.* 317, 1–8.
- Saloranta, T.M., Haugan, P.M., 2004. Northward cooling and freshening of the warm core of the West Spitsbergen Current. *Polar Res.* 23, 79–88.
- Sanchez-Vidal, A., Veres, O., Langone, L., Ferré, B., Calafat, A., Canals, M., Durrieu de Madron, X., Heussner, S., Mienert, J., Grimalt, J.O., Pusceddu, A., Danovaro, R., 2015. Particle sources and downward fluxes in the Eastern Fram Strait under the influence of the West Spitsbergen Current. *Deep Sea Res.* 103, 49–63.
- Sanders, H.L., 1968. Marine benthic diversity: a comparative study. *Am. Nat.* 102, 243–282.
- Seinhorst, J.W., 1959. A rapid method for the transfer of nematodes from fixative to anhydrous glycerine. *Nematologica* 4, 67–69.
- Skogseth, R., Haugan, P.M., Jakobsson, M., 2005. Water mass transformations in Storfjorden. *Cont. Shelf Res.* 25, 667–695.
- Soltwedel, T., 2000. Metazoan meiobenthos along continental margins: a review. *Prog. Oceanogr.* 46, 59–84.
- Szymczak-Zyla, M., Kowalewska, G., 2007. Chloropigments in the Gulf of Gdansk (Baltic Sea) as markers of the state of this environment. *Mar. Poll. Bull.* 55, 512–528.
- Tyler, P., Amaro, T., Arzola, R., Cunha, M.R., De Stigter, H., Gooday, A., Huvenne, V., Ingels, J., Kiriakoulakis, K., Lastras, G., Masson, D., Oliveira, A., Pattenden, A., Vanreusel, A., Van Weering, T., Vitorino, J., Witte, U., Wolff, G., 2009. Europe's Grand Canyon – Nazare Submarine Canyon. *Oceanography* 22, 46–57.
- Vanaverbeke, J., Bezerra, T.N., Braeckman, U., De Groot, A., De Meester, N., Deprez, T., Derycke, S., Gilarte, P., Guilini, K., Hauquier, F., Lins, L., Maria, T., Moens, T., Pape, E., Smol, N., Taheri, M., Van Campenhout, J., Vanreusel, A., Wu, X., Vincx, M., 2015. NeMys: World Database of Free-Living Marine Nematodes. (<http://nemys.ugent.be>) (accessed 25.02.15).
- Van Oevelen, D., Soetaert, K., Garcia, R., de Stigter, H.C., Cunha, M.R., Pusceddu, A., Danovaro, R., 2011. Canyon conditions impact carbon flows in food webs of three sections of the Nazaré canyon. *Deep-Sea Res.* 58, 2461–2476.
- Wadhams, P., 2012. Arctic ice cover, ice thickness and tipping points. *Ambio* 41 (1), 23–33.
- Wadhams, P., Davis, N.R., 2000. Further evidence of ice thinning in the Arctic Ocean. *Geophys. Res. Lett.* 27 (24), 3973–3975.
- Walsh, J.J., 1991. Importance of continental margins in the marine biogeochemical cycling of carbon and nitrogen. *Nature* 350, 53–55.
- Warwick, R.M., Howard, H.M., Somerfield, P.J., 1998. *A Synopsis of the Free Living Marine Nematodes. Part III: Monhysterids*. Field Studies Council, Shrewsbury.
- Weaver, P.E., Billett, D.M., Boetius, A., Danovaro, R., Freiwald, A., Sibuet, M., 2004. Hotspot ecosystem research on Europe's deep-ocean margins. *Oceanography* 17, 132–143.
- Wieser, W., 1953. Die beziehung zwischen mundhöhlengestalt, Ernährungsweise und vorkommen bei freilebenden marinen nematoden. *Ark. Zool.* 2, 439–484.
- Włodarska-Kowalcuk, M., Kendall, M.A., Marcin Węslowski, J., Klages, M., Soltwedel, T., 2004. Depth gradients of benthic standing stock and diversity on the continental margin at a high-latitude ice-free site (off Spitsbergen, 79°N). *Deep-Sea Res.* 51, 1903–1914.
- Zeppilli, D., Sarrazin, J., Leduc, D., Martinez Arbizu, P., Fontaneto, D., Fontanier, C., Gooday, A.J., Kristensen, R.M., Ivanenko, V.N., Sørensen, M.V., Vanreusel, A., Thébaud, J., Mea, M., Allio, N., Andro, T., Arvigo, A., Castrec, J., Danielo, M., Foulon, V., Fumeron, R., Hermabessiere, L., Hulot, V., James, T., Langonne-Augen, R., Le Bot, T., Long, M., Mahabror, D., Morel, Q., Pantalons, M., Pouplard, E., Raimondeau, L., Rio-Cabewillo, A., Seite, S., Traisnel, G., Urvo, K., Van der Stegen, T., Weyand, M., Fernandes, D., 2015. Is the meiofauna a good indicator for climate change and anthropogenic impacts? *Mar. Biodivers.* 45, 505–535.