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Diversity and distribution of cold-seep fauna associated with different geological and environmental settings at mud volcanoes and pockmarks of the Nile Deep-Sea Fan

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Abstract :

The Nile Deep-Sea Fan (NDSF) is located on the passive continental margin off Egypt and is characterized by the occurrence of active fluid seepage such as brine lakes, pockmarks and mud volcanoes. This study characterizes the structure of faunal assemblages of such active seepage systems of the NDSF. Benthic communities associated with reduced, sulphidic microhabitats such as sediments and carbonate crusts were sampled by remotely operated vehicles during two cruises in 2006 (BIONIL) and 2007 (MEDECO). Environmental conditions and biological factors including family-level faunal composition, density and diversity were measured at local and regional scales. Significant differences were detected at different spatial scales: (1) the fauna of reduced habitats differed substantially in activity, diversity and biomass from the non-seep environment at similar water depth, (2) cold seep microhabitats showed differences in community structure and composition related to substratum type as well as to the intensity and location of fluid emissions.

38 Keywords: Nile Deep-Sea Fan; cold seeps; benthic macrofauna; alpha diversity;
39 environmental conditions; chemosynthetic ecosystem; beta diversity.

40

41 1. Introduction

42

43 Since their discovery on the Florida Escarpment in the Gulf of Mexico (Paull et al.
44 1984), cold seeps have been reported along convergent plate boundaries on active
45 as well as passive continental margins, where over-pressure in the sediments
46 controls the emission of fluids enriched in methane or other hydrocarbons to the
47 seafloor and hydrosphere (Milkov 2000; Dimitrov 2002). Depending on their
48 geophysical settings, these cold seeps are associated with distinct geological
49 features such as gas hydrates, pockmarks, brine lakes and mud volcanoes (MVs)
50 (Milkov 2000; Hovland et al. 2002; Judd and Hovland 2007; Foucher et al. 2009). To
51 date, hundreds of seep sites supporting chemosynthesis-based communities have
52 been encountered throughout the world's oceans (Sibuet and Olu 1998; Levin 2005;
53 Campbell 2006; Baker et al. 2010).

54

55 The Eastern Mediterranean Sea is one of the world's MV and pockmark hotspots
56 (Kopf 2002; Foucher et al. 2009). Most of the MVs are associated with the active
57 Mediterranean Ridge that stretches over more than 1500 km (Cita et al. 1981) and
58 the thickly sedimented Nile Deep-Sea Fan (NDSF) along the Mesozoic-rifted
59 continental margin of northern Egypt (Bellaiche et al. 2001; Mascle et al. 2001;
60 Loncke et al. 2004; Mascle et al. 2006). The present study focuses on sites of the
61 NDSF that have been explored since 2003 in the frame of the European Science
62 Foundation (ESF) MEDIFLUX program (2003-2007) and the European 6th
63 Framework Program project HERMES (2005-2009).

64

65 The NDSF is divided into four morpho-structural provinces (Figure 1a): (1) the
66 Levantine province, a domain of salt-related folding; (2) the Eastern province, a
67 domain of intense salt-related tectonics; (3) the Central province with pockmark fields
68 and gas chimneys, distinguished by active sedimentary instability and fluid-related
69 processes; and (4) the Western province with mud cones, characterized by active
70 turbiditic processes, salt tectonics and fluid venting (Mascle et al. 2006; Huguen et al.
71 2009). The accumulation of organic-rich sediments, probably since the early

72 Cenozoic, led to the formation of hydrocarbons in deep reservoirs that were partially
73 sealed by the deposition of thick evaporites during the Messinian (Hsu et al. 1977). A
74 mixture of hydrocarbons, water and mud is expelled through faults that may extrude
75 salt deposits, which reach the seafloor (Loncke et al. 2004). Fluid seepage is
76 recorded in geological features such as mud cones, caldera-like depressions, gas
77 chimneys, brine pools and pockmarks (Gontharet et al. 2007; Bayon et al. 2009a).
78 Chemosynthesis-based communities have been observed in association with these
79 different features (Huguen et al. 2005; Zitter et al. 2005; Dupré et al. 2007).

80

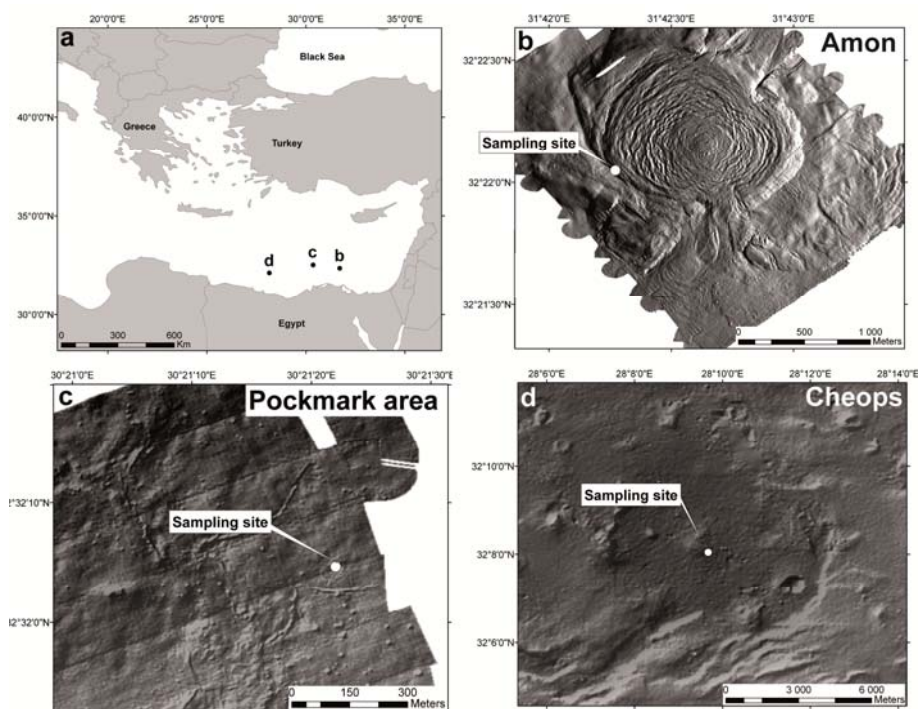


Fig. 1 (a) General map of the Eastern Mediterranean Sea with the localisation of the sampling sites in the three morpho-structural provinces: (b) the Amon mud volcano (MV) located in the Eastern province; (c) the Pockmark area located in the Central province and, (d) the Cheops MV in the Western province. Sampling sites are indicated on each MVs

81

82 Faunal assemblages associated with Mediterranean cold seeps from the NDSF are
83 still relatively unknown. Only those from a few sites along the Mediterranean Ridge
84 have been described, and symbiont-bearing species such as the siboglinid
85 polychaete *Lamellibrachia anaximandri*, the lucinid *Lucinoma kazani* and the mytilid
86 *Idas modiolaefomis* were identified (Salas and Woodside 2002; Olu-Le Roy et al.
87 2004; Werne et al. 2004; Duperron et al. 2008; Southward et al. in press). The
88 distribution of fauna on the Amsterdam MV has been hypothesized to be linked to the

89 amount of methane escaping from the mud flows, which decreases from the summit
90 to the periphery (Olu-Le Roy et al. 2004). Likewise, biological zonation has also been
91 observed on the Barbados prism (Olu et al. 1997) and the Håkon Mosby MV
92 (Niemann et al. 2006; Jerosch et al. 2007). In both cases, the summit of the MV was
93 covered by fresh gassy mud flows and devoid of visible epifauna. Communities
94 dominated by sulphide oxidizing bacterial mats were observed close to the summit,
95 followed by symbiont-bearing fauna and heterotrophic fauna towards the periphery
96 (Olu et al. 1997; Zitter et al. 2003; Niemann et al. 2006; Jerosch et al. 2007). Fresh
97 mud flows are often characterized by very high rates of upward flux of reduced
98 sulphidic fluids, excluding animals (de Beer et al. 2006). Older mud flows, located at
99 the periphery, transport lower concentrations of methane and sustain sulphide
100 production, fueling chemosynthetic populations of siboglinid tubeworms or bivalves
101 like *Acharax*. The latter migrate to deeper sediment layers to reach for reduced
102 chemical compounds. This environment also constitutes a favorable habitat for
103 heterotrophic fauna, which develop in response to a local increase in microbial
104 production (Levin and Mendoza 2007).

105

106 The present study was the first opportunity to characterize the structure of the faunal
107 assemblages in the NDSF seeps on two types of geological features: MVs and
108 pockmarks. Prior to 2006, no ecological study had been performed on NDSF seep
109 sites, with the exception of a few observations and samples taken during the
110 NAUTINIL cruise in 2003 (Dupré et al. 2007; Bayon et al. 2009b; Huguen et al.
111 2009). The macro- and meiofaunal benthic communities associated with different
112 microhabitats found in three provinces of the NDSF were sampled by remotely
113 operated vehicles (ROVs) during two cruises: BIONIL in 2006 and MEDECO in 2007.
114 The microhabitats were characterized with regard to their environmental conditions
115 and faunal communities, mostly to family level. We then compared faunal
116 composition, density and diversity at local and regional scales to test the hypotheses
117 that 1) reduced habitats support higher biomasses but lower diversity of meio- and
118 macrofauna compared to surrounding oxygenated habitats, 2) carbonate crusts and
119 reduced sediments bear different faunal assemblages, 3) faunal composition is
120 related to microhabitat type rather than to the larger geological setting, 4) beta
121 diversity between the different microhabitats is related to differences in fluid flow and
122 substratum type.

123

124 2. Materials and methods

125 Faunal sampling and habitat characterizations were done during BIONIL M70/2b
126 aboard the German R/V *Meteor* with the ROV *Quest4000* (MARUM, University
127 Bremen) in November 2006 and during leg 2 of MEDECO aboard the French R/V
128 *Pourquoi Pas?* with the ROV *Victor6000* (Ifremer) in November 2007.

129

130 2.1. Study sites

131 The cold seep sites from three of the four provinces of the NDSF were investigated:
132 1) the Amon MV in the Eastern province; 2) a carbonate cemented area close to a
133 pockmark field associated with large debris-flows in the Central province; and 3) the
134 Cheops MV in the Western province hosting large brine pools (Figure 1). A single
135 reference sample located 15 km away from the centre of the Amon MV and outside
136 the influence of fluid emissions, was sampled as a reference (hereafter marked "Ref")
137 for oxygenated deep-sea sediments not associated with fluid flow.

138

139 2.1.1. The Western province – the Amon MV

140 The Amon MV (32°22'05"N – 31°42'27"E, Figure 1b) is circular, approximately 3 km
141 in diameter, and 90 m high. It lies close to the limit of the Messinian platform, at 1150
142 m water depth. The summit is covered with mud blocks and clasts and shows a
143 disturbed, chaotically structured surface suggesting recent impacts of mud extrusion
144 and gas expansion. Temperatures at the centre reach 45°C at 10 m below the
145 seafloor, confirming high upward fluid flow at this MV (Dupré et al. 2007; Dupré et al.
146 2008). The periphery of the Amon MV is characterized by highly bioturbated
147 hemipelagic sediments. At its south-western rise, a lateral flow of reduced muds was
148 identified ('sulphur-band') surrounded by carbonate crusts that were both sampled in
149 2006 during BIONIL. The carbonate crusts were rather thick, we could not observe
150 blackish muds or siboglinid colonies associated with them.

151

152 2.1.2. The Central province – the Pockmark area

153 The Central province hosts large carbonate-cemented areas associated with reduced
154 debris-flows, and numerous small pockmarks located between 1700 and 2100 m
155 depth (Figure 1c). The pockmarks form circular depressions of a few meters in
156 diameter and about 1 m deep, and are associated with the presence of authigenic

157 carbonate crusts and reduced sediments (Loncke et al. 2004). During BIONIL,
158 benthic communities were sampled from one reduced blackish sediments site at mid-
159 slope (site 2A, 32°32'00"N – 30°21'10"E, 1700 m) as well as from their surrounding
160 carbonate cements. These were directly associated with blackish muds, and living
161 siboglinid colonies were observed between the cracks of the flat, thin carbonates.

162

163 2.1.3. The Eastern province – the Cheops MV

164 The Cheops MV is located within the Menes caldera at 3000 m depth (32°08'05"N –
165 28°09'67"E, Figure 1d), above the Messinian platform. This caldera is a circular 50 m
166 deep depression 8 km in diameter. As previously observed in 2003 during the
167 NAUTINIL cruise, a mixture of brine and mud was flowing from Cheops during the
168 sampling operations in 2007 (MEDECO). The mud is expelled from deep layers as
169 indicated by high temperature anomalies (Huguen et al. 2009). This MV is also
170 characterized by numerous brine pools, covered by bright white matter, identified as
171 microbial sulphur deposits (Dupré et al. 2007; Omoregie et al. 2008). Brine pools
172 constitute direct evidence of fluid emissions, and the migration of fluids enriched in
173 salt induces high sediment instability that may influence faunal composition and
174 distribution on this MV. Faunal sampling and environmental characterizations were
175 carried out during MEDECO. Sparse carbonate crusts were observed but not
176 sampled.

177

178 2.2. Description of the microhabitats

179 At all cold seep sites visited, ROV surveys indicated a mosaic of visually
180 distinguishable microhabitats, characterized by the presence of visible fauna or
181 microbial mats. Two types of reduced habitats were sampled: 1) reduced blackish
182 sediments (Red) covered with whitish bacterial mats or small tubeworms at the
183 surface (Figures 2a, c, e) and 2) carbonate crusts (CC) that were dark-colored at
184 Amon, or “crumbly” and of whitish to light grey color at the Pockmark area Figures
185 2b, d).

186

187 Chemical characterization of the microhabitats was performed above the reduced
188 sediments of Cheops MV during MEDECO. Water samples were taken for chemical
189 analyses using the PEPITO water sampler above the organisms as close as possible
190 to the seafloor using the *Victor6000* manipulator arm. PEPITO collects water in 200

191 ml titanium bottles (Sarradin et al. 2009). Chemical measurements and sediment
192 samples were taken during BIONIL as close as possible above the seafloor or in soft
193 sediments with bottles (750 ml) and push cores (inner diameter 7.5 cm) at 2.5 to 50
194 m from the sampled microhabitats. Further sampling details are given in Table 1.
195

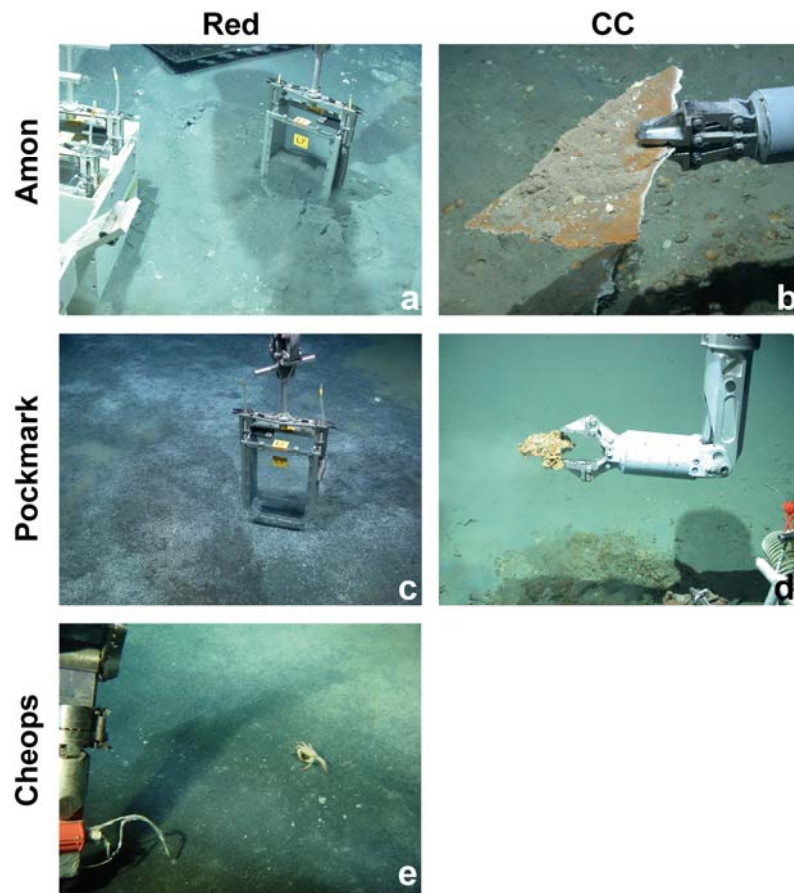


Fig. 2 Representative photographs of the microhabitats sampled in the three study sites. On the Amon MV: (a) reduced sediments and (b) carbonate crusts; in the Pockmark area: (c) reduced sediments and (d) carbonate crusts; on the Cheops MV: (e) reduced sediments. Red: reduced sediments CC: carbonate crusts. All microhabitats were sampled during the BIONIL (2006) and MEDECO (2007) cruises. Photos a, b, c, d: MARUM, University Bremen, *QUEST4000* and photo e: Ifremer, *Victor6000*

196

197 Epi- and endofauna were sampled with blade corers on a surface of 200 cm² (Menot
198 et al. 2010) on all soft sediment sites (Figures 2a, c, d, g) and pieces of carbonate
199 crusts were sampled using the claw of the ROV *Victor6000* (Figures 2b, e). A
200 reference site 15 km away from the active centre of Amon has been sampled with a
201 single multicorer on which 3 tubes of a surface of 74 cm² were sampled (pseudo-
202 replicates). The number of samples for each microhabitat is reported in Table 1.

203 Quantitative sampling of the crusts was difficult because they had to be broken off in
204 pieces with the submersible manipulator. No crusts were obtained from Cheops.

205

206 2.3. Physico-chemical analyses

207 The 200 ml water samples were used to determine methane concentrations using the
208 technique of headspace sampling gas chromatography with a thermal-conductivity
209 detector (TCD) and a flame-ionisation detector (error of 4%; see method in Sarradin
210 and Caprais 1996).

211

212 Sediments from push corers were split horizontally at 1 cm intervals on board and
213 porewater was extracted by centrifugation of the different sediment layers. After
214 filtration and dilution, sulphate and chloride concentrations were measured by non-
215 suppressed anion exchange chromatography (Water IC-Pak anion exchange column,
216 waters 430 conductivity detector). Total dissolved sulphide concentrations were
217 determined with the diamine complexation method by colorimetric method (Cline
218 1969). Intact cores, along with supernatant water, were used for pH, oxygen and total
219 dissolved sulphide concentration measurements. Small-scale porewater
220 concentration profiles for O₂, H₂S, and pH were performed on push core samples
221 from soft sediments using microelectrodes as described in de Beer et al. (2006).
222 Microelectrodes with a tip diameter of ca. 20 µm were lowered into the sediment with
223 a step resolution of 200 µm to monitor the concentration profiles within the upper
224 sediment layer. Total oxygen consumption was measured *in situ* using a ROV-
225 operated benthic chamber module (Treude et al. 2009). The chamber encloses an
226 area of ca. 285 cm² together with approximately 10-15 cm of overlying bottom water.
227 The change in O₂ concentration over time in the enclosed water volume was
228 continuously monitored by two Clark-type mini-electrodes mounted in the chamber
229 lid. This measurement integrates all relevant transport and consumption processes
230 (diffusion, advection and fauna mediated transport as well as fauna respiration).

231

232 2.4. Faunal sorting and identification

233 The faunal samples were processed as described in Ritt et al. (2010). Sediments
234 from blade corers were photographed and split horizontally (0-1, 1-3, 3-5, 5-10, >10
235 cm) immediately after recovery. The range of the last slice depended on core lengths
236 that varied from 10 to 20 cm (Table1). Core slices were passed through a sieve

237 column (2 mm, 1 mm, 500 μm , 250 μm) and the retained sediment was preserved in
238 10% buffered formalin. In the laboratory, all sediments up to 10 cm below the
239 seafloor were rinsed and invertebrates were sorted under a dissecting microscope
240 and identified to the lowest taxonomic level possible (here mostly family level). In this
241 study, we considered macrofauna *sensu stricto* (>250 μm , Hessler and Jumars
242 1974), and any meiofaunal taxa such as Nematoda, Copepoda, Ostracoda and
243 Acarina were analysed separately. As a consequence, meiofaunal samples contain
244 only the largest fraction retained by a 250 μm mesh, and do not include the 32 μm or
245 62 μm size limit usual for meiofauna (Hessler and Jumars 1974; Thistle 2003; Van
246 Gaever et al. 2006).

247

248 The CC samples were preserved individually in 10% buffered formalin on board after
249 recovery. In the laboratory, the carbonates crusts were treated individually by
250 retrieving the organisms embedded or attached on them without breaking the
251 carbonate crusts. Then they were washed over a 250 μm mesh and the organisms
252 retained were processed as those on the soft sediments. The surface of the sampled
253 carbonate crusts were estimated using the IPLab Spectrum® image analysis
254 software. Quantitative 2-D surface analyses were performed on video images of the
255 upper face of the crusts, and we did it thrice to reduce error resulting from on-screen
256 tracing (Sarrazin and Juniper 1999). Total surface area was used to calculate area-
257 related indicators, such as density and biomass by counting organisms at both faces
258 and in the holes but divided the total of individuals only by the surface area.
259 However, because it does not take topography into account, this method may
260 underestimate total surface area and in turn overestimate density and biomass. The
261 crusts from the Pockmark area had a more complex topography with numerous holes
262 in comparison with the flat carbonates from Amon, hence, the two-side method may
263 have added to the uncertainty with areal estimates in this case.

264

265 2.5. Vertical distributions

266 Vertical distributions within each reduced sediment microhabitat and the reference
267 site were studied in the depth layers 0-1, 1-3, 3-5 and 5-10. Densities were calculated
268 by summing up the sediment layers up to 10 cm below the seafloor. This was
269 repeated for relative abundance and biomass. Biomass was assessed by measuring
270 the mean preserved wet weight (pww) for each microhabitat. To do so, individuals of

271 all major macrofaunal taxa (bivalves, polychaetes, gastropods and crustaceans) were
272 pooled, pat-dried on absorbent paper and weighed on a microbalance with an error
273 of 0.1 mg.

274

275 2.6. Diversity measurements

276 Within-microhabitat (α -diversity) and between-microhabitat (β -diversity) diversity
277 (Whittaker 1960; Gray 2000) were estimated for all microhabitats.

278

279 2.6.1. Alpha-diversity

280 The α -diversity analyses were performed at the family level, which was reached for
281 most of the taxa except Zoantharia, Scyphozoa, Terebellida, Isopoda, Leptostraca,
282 Nematoda and Acarina. Undetermined families, individuals and larvae were removed
283 from the analysis because of the probability that they belong to a family already
284 listed. This may have resulted in an underestimation of the taxonomic richness.
285 Sample-based rarefaction curves (*sensu* Gotelli and Colwell 2001) were calculated
286 on macrofaunal datasets for each of the three study sites (Sanders 1968). Individual-
287 based rarefaction curves were also computed on macrofaunal datasets for each
288 microhabitat type, regardless of the province of origin. These curves plot expected
289 taxonomic richness against sampling effort and allow comparisons impossible with
290 observed richness (S). All rarefaction curves use the expected number of individuals
291 as the X-axis (Sanders 1968, corrected and modified by Hurlbert 1971; Gotelli and
292 Colwell 2001; Gauthier et al. 2010). Observed within-microhabitat taxonomic diversity
293 was evaluated using common diversity indices as well as more robust intrinsic-
294 diversity-based ordering methods (Liu et al. 2007; Gauthier et al. 2010). Commonly
295 used to define the α diversity, the taxonomic richness (S), the number of taxonomic
296 groups observed in each microhabitat, the Shannon's entropy (H'_e ; Shannon 1948)
297 and the Gini-Simpson diversity index (D_{GS} ; Gini 1912; Simpson 1949) were
298 calculated. They are presented along with their *numbers equivalents*, allowing
299 straightforward comparisons between communities (Hill 1973; Patil and Taillie 1982;
300 Jost 2006; Jost 2007). Community evenness was also determined using Pielou's
301 index of evenness (J' ; Pielou 1969).

302

303 The right tail-sum method (RTS) is a diversity ordering method, which is more robust
304 and stringent than other methods and allows graphical comparisons of communities
305 (Patil and Taillie 1982; Tothmérész 1998; Liu et al. 2007). Communities are ordered
306 in decreasing diversity from the top most curves to the lowest ones. No clear
307 conclusions can be drawn when curves intersect (Liu et al. 2007).

308

309 2.6.2. Beta-diversity

310 Despite the modest number of samples, multivariate analyses were conducted to
311 better illustrate the similarities and differences among faunal samples. The lowest
312 available taxonomic level was used. Principal component analysis (PCA) and Ward's
313 hierarchical clustering were used to indirectly evaluate the influence of habitat
314 conditions on community structure variation within and between the different
315 microhabitats and sites, but excluding the undetermined taxa as previously explained
316 for the alpha-diversity. A Procrustean randomization test (Jackson 1995) was
317 performed to compare the PCA results of the macrofaunal and meiofaunal datasets.
318 Abundance data were first Hellinger-transformed to conserve Hellinger, rather than
319 Euclidian, distances in PCA (Legendre and Gallagher 2001). Hellinger distances
320 were also used for Ward's hierarchical clustering. This distance gives low weight to
321 rare taxa in the analyses. In marine ecology in general, and even more so in the
322 deep-sea, rare species are not well sampled, and their sporadic appearance in
323 samples is mostly attributable to sampling error. In the PCA, the equilibrium
324 contribution circle was computed to identify the taxa having the most impact on the
325 position of the samples in the ordination (Legendre and Legendre 1998).

326 The Jaccard's similarity coefficient (S_{jacc}) was used to quantify similarity in terms of
327 shared taxa among replicates within each microhabitat (Jaccard 1901); giving equal
328 weight to all taxa. Mean Jaccard similarity was computed to evaluate within-
329 microhabitat variation.

330

331 All analyses were performed in the R environment (R, Development Core Team,
332 2009). Rarefaction curves, diversity indices and diversity profiles were computed both
333 with the Biodiversity R package (Kindt and Coe 2005) and functions in Gauthier et al.
334 (2010). Multivariate analysis was carried out using the vegan package (Oksanen et
335 al. 2008).

336 3. Results

337 3.1. Physico-chemical characterization of microhabitats

338 The length of the cores varied from 10 to 20 cm depending on the nature of the
339 substratum (Table 1). All samples came from surface cold seep habitats at *in situ*
340 bottom water temperature of 13.5°C, as at the reference site. The Red cores from the
341 Pockmark area contained black sediments with a strong hydrogen sulphide odor. At
342 Amon, a horizon of 8-10 cm of black sediments overlaid grayish to beige hemipelagic
343 sediments. On Cheops, a black layer of only 1-2 cm was found on top of beige
344 hemipelagic sediments. The cores of the reference site contained only beige
345 sediments.

346

347 3.2. Chemical characterization at a larger scale around microhabitats

348 3.2.1. Bottom water measurements

349 Overall, the pH was slightly lower in reduced sediments than at the reference site
350 (Table 2). According to microprofiler measurements, pH value reached 7.9 at the
351 interface of reduced sediments on Amon while in the Pockmark area, it was around
352 8.1 (Table 2).

353

354 Oxygen bottom water concentrations were similar at all sites, including the reference
355 site (200-230 $\mu\text{mol l}^{-1}$) with the exception of the reduced sediments at Amon, where a
356 temporary depletion was observed, reaching values below 200 $\mu\text{mol l}^{-1}$. No free
357 sulphide was detected in the bottom waters at any of the sites, but sulphide was
358 found within the porewaters at two reduced sediment sites (Table 2). Low
359 concentrations of methane were measured in the bottom waters of Cheops and the
360 Pockmark area while they ranged between 3.6 and 9.3 $\mu\text{mol l}^{-1}$ in the overlying water
361 of Cheops samples (Table 2).

362

363 Sulphate values of 31 mmol l^{-1} and chloride values of 529 mmol l^{-1} were measured
364 above and throughout the core from the reference site. Sulphate and chloride
365 measurements above the reduced sediments on Amon showed values varying from
366 30 to 40 mmol l^{-1} and 404 to 580 mmol l^{-1} respectively (Table 2). Here, spatial
367 heterogeneity between samples was high, despite the proximity of the cores (few dm,
368 e.g. PC 46 and PC 47). In microbial mats from the Pockmark area, sulphate

369 concentrations varied from 29 to 30 mmol l⁻¹ while chloride values were high, ranging
370 from 606 to 630 mmol l⁻¹ (Table 2).

371

372 3.2.2. Porewaters, oxygen consumption and sulfate reduction rates in sediments

373 Oxygen penetration depth measured by microsensors was >4 cm at the reference
374 site (Table 2). The porewater samples from the reference site did not contain
375 sulphide or methane. Accordingly, sulphate reduction rate at the reference site was
376 not measurable, and oxygen consumption was <1 mmol m⁻² d⁻¹ (Table 2).

377

378 In contrast, oxygen microsensor profiles in reduced sediments of Amon, Cheops and
379 the Pockmark area showed complete oxygen consumption within the first 1-2
380 millimeters of seafloor (Figures 3a, b). Total dissolved sulphide profiles in reduced
381 sediments of Amon showed a maximum concentration of 2.5 mmol l⁻¹ at 12 cm depth
382 and were <0.8 mmol l⁻¹ in the top 5 cm (Table 2, Figure 3c). The profile suggested
383 that sulphide was oxidized completely within the first millimeters of sediment. In the
384 Pockmark area, sulphide concentrations at 12.5 cm depth reached 25 mmol l⁻¹
385 (Figure 3d), but sulphide was also completely consumed within the surface
386 sediments (Table 2). No porewater data were available for Cheops due to limitation in
387 dive time.

388

389 At the reference site off Amon, sulphate and chloride concentrations were
390 homogeneous along the whole length of the core with a mean of 32±2.4 mmol l⁻¹ for
391 sulphate and 530±49.5 mmol l⁻¹ for chloride (Figure 4a). On Amon reduced
392 sediments, sulphate and chloride profiles were homogeneous along the length of the
393 core reaching values similar to the reference sample with the exception of a high
394 sulphate concentration at the top of the core (Figure 4b). In the Pockmark area, the
395 consumption of sulphate was visible throughout the 16 cm of the core length,
396 whereas lower variation was observed in chloride (Figure 4c).

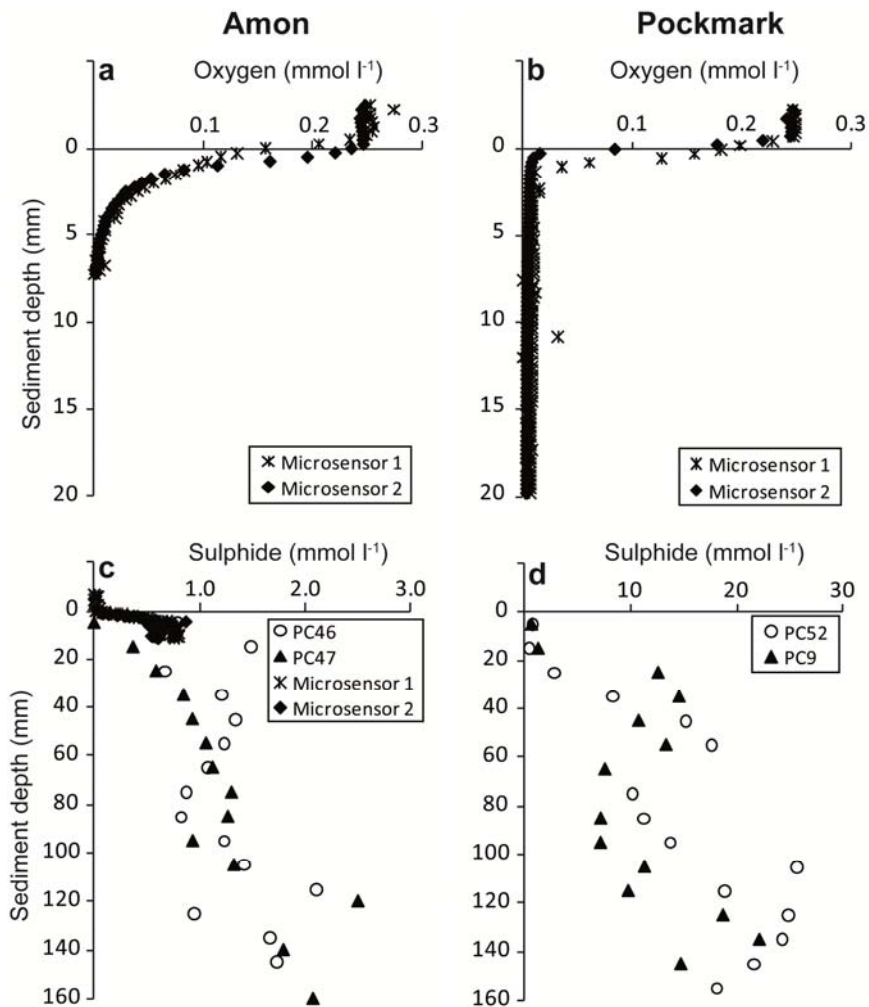


Fig. 3 (a, b) Dissolved oxygen and (c, d) sulphide profiles measured by microsensors and in pore water extracted from push corers (PC) taken in reduced sediments on the (a, c) Amon MV and in (b, d) bacterial mats covering reduced sediments in the Pockmark area. The measurements were performed during the BIONIL cruise (2006)

397

398 Integrated sulphate reduction rates were negligible at the reference site, and low at
 399 the reduced sediment of Amon. Intermediate rates were measured for Cheops and
 400 high rates associated with the Pockmark area (Table 2). Likewise, total benthic
 401 oxygen fluxes were very low at the reference site, and 1-2 orders of magnitude higher
 402 at all reduced sediment sites, with the highest rates associated with the black
 403 sediments of the Pockmark area (Table 2).

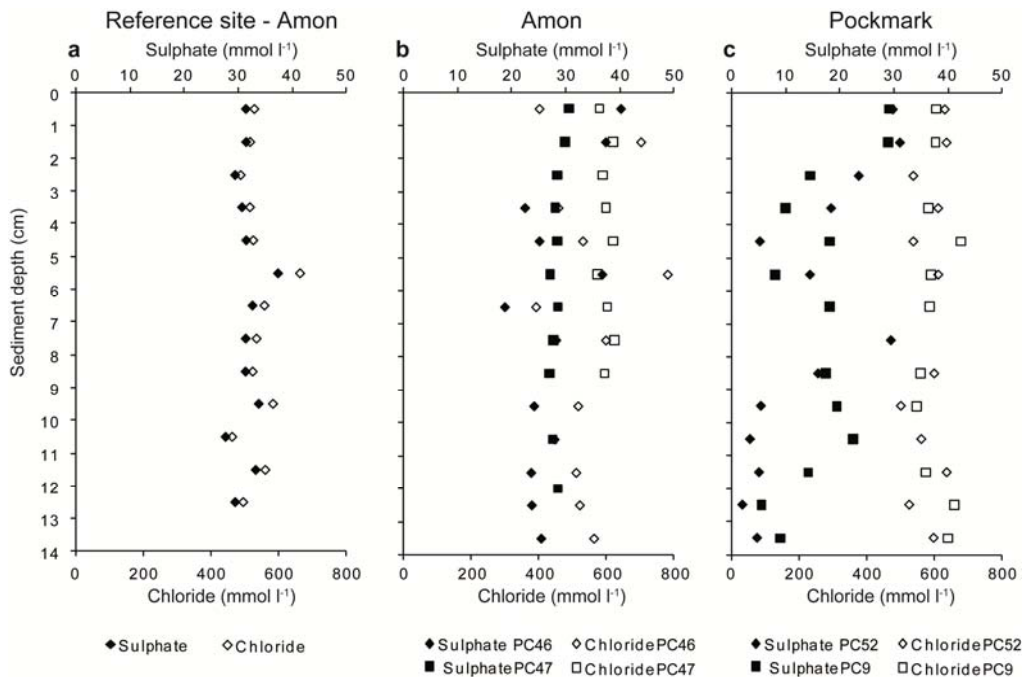


Fig. 4 Sulphate and chloride profiles measured in porewater extracted from sediment cores sampled (a) at the reference site off Amon MV, (b) in reduced sediments on the Amon MV and, (c) in bacterial mats covering reduced sediments in the Pockmark area. The measurements were performed during the BIONIL cruise (2006)

404

405

406 3.3. Macro- and meiofaunal community description

407 3.3.1. Composition, abundance, density and α -diversity patterns

408

409 Mean macrofaunal densities varied from 650 to 2,100 individuals m^{-2} at Amon (Table
 410 3), 1,950-3,500 individuals m^{-2} in the Pockmark area (Table 43) and from 3,200 to
 411 5,250 individuals m^{-2} at Cheops (Table 4). This represents approximately 3.5%, 55%,
 412 and 78% of the total fauna sampled at each site (Tables 5, 6). In comparison, the
 413 fully oxic reference site had from 541 to 1,081 macrofaunal individuals m^{-2} (Table 3),
 414 which represented 67% of the total fauna. On the carbonate crust microhabitat (CC),
 415 densities varied from 1,852 to 7,353 individuals m^{-2} at Amon (Table 3) and from
 416 1,852 to 7,353 individuals m^{-2} in the Pockmark area (Table 4) representing
 417 respectively 100% (except CC2 where it only represent 20%) and 63% of the fauna
 418 sampled (Tables 3, 4).

419

420 Despite the large sieve mesh size used (250 μm), many specimens corresponding to
 421 meiofaunal groups (copepods, ostracods, nematodes, mites) were found in our
 422 samples (Tables 5, 6). Mean densities of meiofauna $>250 \mu m$ varied from 31,800 to

423 75,550 individuals m⁻² at Amon (Table 5), 1,450 to 3,950 individuals m⁻² in the
424 Pockmark area (Table 6) and reached 600 to 2,850 individuals m⁻² at Cheops (Table
425 6). At Amon, meiofaunal mean density was higher in reduced sediments compared to
426 carbonate crusts (Table 5). Overall, nematodes dominated the meiofauna >250µm
427 samples, varying from 95 to 100% of total abundances on the reduced sediments
428 from the Amon and Cheops (Tables 5, 6). However, in the reduced sediments of the
429 Pockmark area, nematodes represented only 36% of the meiofauna (Table 6). Here,
430 harpacticoid copepods reached up to 37.5% of the meiofaunal abundance, followed
431 by ostracods (~16%). Surprisingly, besides four nematodes, no meiofauna was
432 sampled from the CC microhabitat of Amon, compared to a relatively high number of
433 nematodes found at the CC of the Pockmark area (Tables 5, 6).

434

435 Relative faunal abundances varied between microhabitats and between replicate
436 samples of the same microhabitat, especially on carbonate crusts. Overall, the
437 steady increase of the individual-based rarefaction curves suggests that the sampling
438 effort was not sufficient (Figure 5a). Only the curves of the reduced microhabitats of
439 Cheops and the Pockmark area showed that we attained a relatively good estimation
440 of their taxonomic richness. These curves also showed that the taxonomic richness
441 between the different reduced sediment microhabitats was highest on Amon,
442 followed by the Pockmark area and finally Cheops. The opposite trend was observed
443 for the CC microhabitats, where the diversity was higher in the Pockmark area
444 (Figure 5a). Since the ranking of the curves would probably remain the same with
445 additional macrofaunal samples, we can conclude with confidence that the total
446 family richness (S) on Amon was highest on reduced sediments, intermediate on the
447 Reference site and lowest on CC, while the CC microhabitat in the Pockmark area
448 was richer than the reduced sediments (Figure 5a; Tables 7, 8).

449

450 In terms of evenness (Pielou's index J', Table 8), the reference sample harbored the
451 most even distribution followed by CC from the Pockmark area and reduced
452 sediments from Amon (also shown in Figure 5b). Finally, Red from Cheops was the
453 poorest microhabitat sampled in the NDSF. It was amongst the least even of all
454 microhabitats along with CC from Amon and Red from Pockmark (Tables 7, 8). At
455 Amon, polychaetes were the dominant taxa in the reduced habitats and reference
456 samples, constituting respectively ~82% and 71% of total faunal abundance. A total

457 of 8 polychaete families or orders (since the Terebellida were not identified at the
 458 family level) were represented in the reduced sediments (Tables 3, 7). With ~11.5%
 459 of the total macrofaunal abundance, bivalves were the second dominant taxon in the
 460 reduced sediments of Amon, whereas cnidarians (~18%) ranked second in the
 461 reference sample. Gastropods and crustaceans were present in low abundance
 462 (<6%) in reduced sediments while on the reference samples, low abundances were
 463 for the crustaceans and sipunculians. On CC from Amon, cnidarians represented
 464 72% of the total abundance, distantly followed by polychaetes (~17%; Table 8).
 465 Some gastropods and sipunculians were also present in low abundance (<6%; Table
 466 3a). In the Pockmark area, reduced sediments were dominated by 8 polychaete taxa,
 467 reaching ~84% of the total macrofaunal abundance, followed by bivalves and
 468 gastropods (Tables 4, 7). Contrary to Amon, the fauna from CC in the Pockmark area
 469 was more evenly distributed with gastropods and polychaetes representing
 470 respectively ~51% and 40% of the total abundance (Table 4). Bivalves and
 471 crustaceans were also present, representing less than 8% of the total macrofaunal
 472 abundance (Table 4). The rarefaction curves and the Pielou's index confirm the
 473 higher evenness of the CC from the Pockmark area compared to CC from Amon
 474 (Figure 5a; Tables 7, 8), the highest evenness being observed on the reference site
 475 (Table 8). Finally, on Cheops, polychaetes largely dominated reduced sediments,
 476 with a mean of 96% of the faunal abundance, followed by low proportions of
 477 crustaceans and gastropods (Tables 4, 7).

478

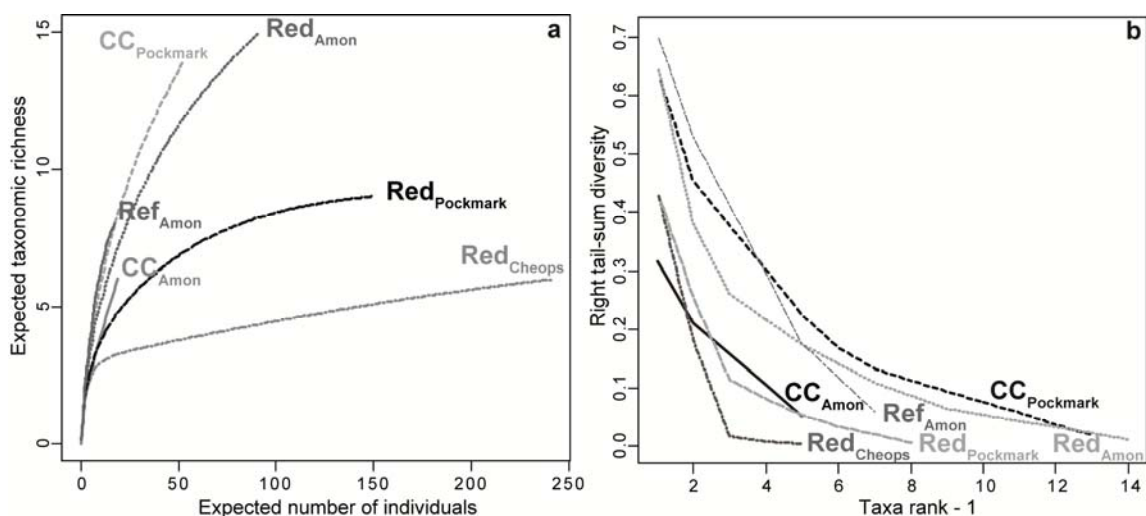


Fig. 5 (a) Rarefaction curves (b) and right tail-sum intrinsic diversity profiles for the pooled macrofaunal abundance data at the family level and at each microhabitat from the Amon MV (3 microhabitats including the reference sample), the Pockmark area (2 microhabitats) and the Cheops MV (1 microhabitat)

479 The RTS performed with the same dataset is difficult to interpret due to the crossing
 480 of the curves (Figure 5b). Using this analysis, Amon reduced sediments were the
 481 richest and most even microhabitat among the three reduced sediments. In contrast,
 482 the CC from the Pockmark area was more diverse than that from Amon (Figure 5b).
 483
 484 Finally, we pooled the data obtained for the different microhabitats to determine the
 485 diversity of each site, including the reference samples from Amon. For Amon and the
 486 Pockmark area, the sample-based rarefaction curves did not level-off, suggesting
 487 that sampling was insufficient to accurately estimate taxonomic richness (Figure 6a).
 488 At Cheops, despite the low sample number (n=3), the curve leveled-off, suggesting
 489 that its macrofaunal diversity was well described (Figure 6a). Our data indicate that
 490 diversity was higher at microhabitats sampled on Amon, followed by the Pockmark
 491 area, the reference samples from Amon and lastly, by Cheops (Figure 6a). Overall,
 492 the distribution of macrofauna was relatively even on Amon, since the most abundant
 493 taxon only reached ~30% for both active and reference sites, whereas the most
 494 abundant taxon represented ~45% and ~55% on the Pockmark area and Cheops
 495 respectively (Figure 6b).

496
 497

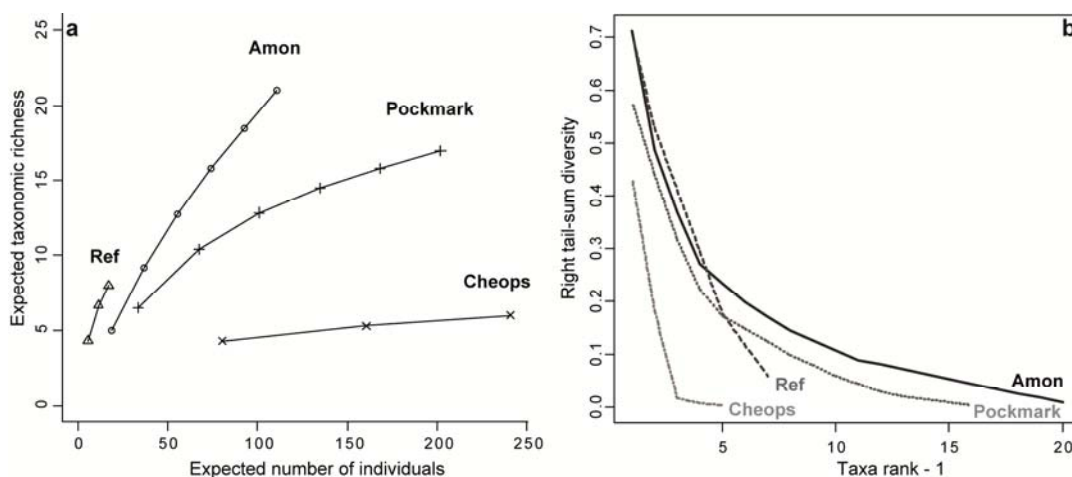


Fig. 6 (a) Rarefaction curves and (b) right tail-sum intrinsic diversity profiles for the pooled macrofaunal abundance data at the family level, according to the three study sites after pooling active microhabitats. Amon MV, n=6, Pockmark area n=3, and Cheops MV, n=3. The reference sample from Amon is reported separately, n=3 (Ref)

498
 499
 500
 501

502 3.3.2. Symbiont-bearing fauna versus heterotrophic fauna

503 The symbiont-bearing fauna (for types of symbioses see Olu-Le Roy et al. 2004)
504 represented 17 to 36% of the total faunal abundance in the reduced sediments from
505 Amon, while the CC and the reference sample did not harbour any (Tables 7, 8). The
506 symbiont-bearing fauna was represented by Frenulata polychaetes as well as by four
507 bivalve species (*Lucinoma kazani*, *Idas modiolaeformis*, *Thyasira striata* and
508 *Isorropodon perplex*; Table 3). The Pockmark area had between 10 and 16% of
509 symbiont-bearing fauna both in the sediment and CC microhabitats, respectively
510 (Tables 5, 7, 8). This fauna was represented by two known bivalve species (*L. kazani*
511 and *I. perplexum*) and one unknown Lucinidae in the sediments. Only one bivalve
512 species was present in the CC microhabitat (*I. modiolaeformis*; Table 4). No
513 symbiont-bearing fauna was sampled at Cheops (Tables 7, 8) or at the reference
514 site.

515

516 3.3.3. Vertical distributions within the sediments

517 The distribution within the sediment layers down to 10 cm below the seafloor of the
518 macrofaunal relative abundances differed between the three reduced sediment
519 microhabitats (Figure 7a). At all reduced sediment sites, oxygen did not penetrate
520 deeper than a few mm, and sulfide concentration increased with sediment depth
521 below 2 cm to 1-2 mmol l⁻¹ at Amon and to 10-20 mmol l⁻¹ in sediments of the
522 Pockmark area. Hence, in the Pockmark area, the macrofauna was concentrated at
523 the uppermost layer [0-1 cm] with about 85% of the total abundance (Figure 7a).
524 However, some capitellid polychaetes and undetermined bivalves – that may be
525 vesicomids and lucinids – were found in the [5-10 cm] layers. In the Cheops area,
526 the macrofauna was almost evenly distributed between the [0-1 cm] and [1-3 cm]
527 layers and only few spionid polychaetes were found in the [5-10 cm] layer. The profile
528 obtained for the reduced sediments of Amon was different, with a more
529 homogeneous distribution within the 10 cm layer and a relatively high abundance at
530 [5-10 cm] (Figure 7a) especially of frenulate, capitellid and dorvilleid polychaetes. At
531 the reference site, most macrofauna was concentrated in almost equal proportions in
532 the two first layers [0-1 cm] and [1-3 cm]. There, the distribution showed a clear
533 decrease with depth, as no organism was found at the [5-10 cm] layer (Figure 7a).
534 The meiofauna >250 µm also decreased with depth at the reference site, with up to
535 60% of the total meiofaunal abundance found in the two first layers (Figure 7b). The

536 same trend was observed in reduced sediments from Amon with this time almost
 537 60% concentrated in the first layer. This pattern was different at the Pockmark area,
 538 where the meiofaunal abundance was highest in the [3-5 cm] layer followed by the [1-
 539 3 cm] and [5-10 cm] layers (Figure 7b). However, the few organisms found in the [5-
 540 10 cm] layer consisted of nematodes at Amon, and of harpacticoid copepods at the
 541 Pockmark area.

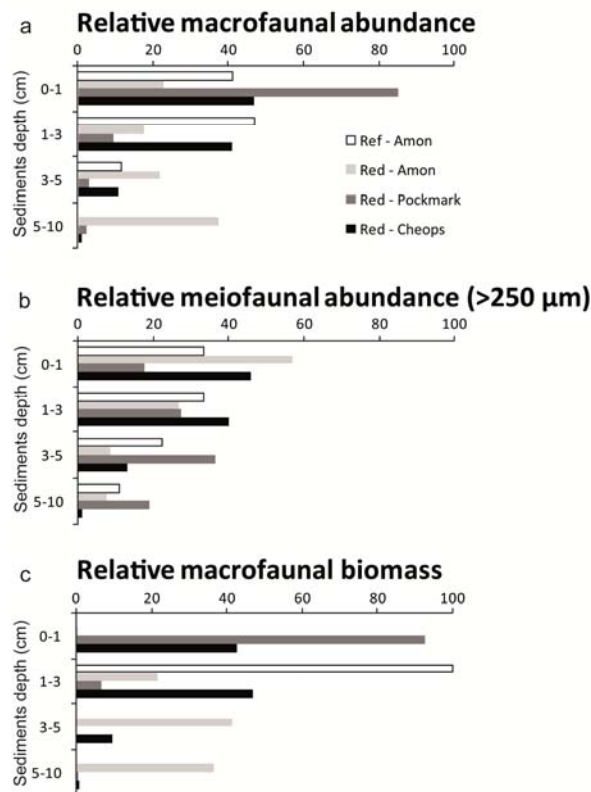


Fig. 7 Vertical distribution of (a) macrofaunal and (b) meiofaunal (>250 µm) relative abundances and (c) macrofaunal relative biomass with depth after summing the three replicates (n=3) for each sediment layer of the reduced sediment microhabitats from Amon MV, Pockmark area and Cheops MV. The reference site from Amon is also included

542

543 In general, all soft sediments showed a low macrofaunal biomass, except the
 544 reduced sediments of Amon where the mean biomass reached 0.12 ± 0.1 kg pww m^{-2}
 545 (Table 7). Here, the vertical distribution showed an increase with depth from 1 to 10
 546 cm with about 40% of the total macrofaunal biomass remaining in the [5-10 cm] layer
 547 (Figure 7c) due to the presence of few lucinid and thyasirid bivalves. In the reduced
 548 sediments of the Pockmark area, most of the macrofaunal biomass (93%) was
 549 observed within the top layer [0-1 cm] and mainly consisted of dorvilleid polychaetes.
 550 Reduced sediments at Cheops hosted a similar biomass in the top two layers [0-1]

551 and [1-3 cm], with 43 and 47% of the total biomass respectively mainly represented
552 by hesionid, spionid, terebellid polychaetes and Leptostraca crustaceans. Next, a
553 sharp decrease was observed with depth (Figure 7c). At the reference site, mean
554 biomass was very low (Table 8), and integrally located within the [1-3 cm] layer
555 (Figure 7c) due to the presence of one sipunculian and few spionid polychaetes.

556

557 3.3.4. Beta diversity patterns

558 The first two components of the principal component analysis (PCA) on macrofaunal
559 data accounted for 41.7% of the variance in macrofaunal distribution (Figure 8a).
560 Three clusters appear in reduced space: the carbonate crust samples; the reduced
561 sediment samples except those from Cheops; and the Amon reference site and
562 Cheops reduced sediments samples. Thus the variability between microhabitats was
563 higher than that within the microhabitats, but lower than that among the geostructures
564 (Figure 8). Polychaete taxa (Spionidae, Terebellida, Dorvilleidae, Capitellidae) and
565 gastropods (Orbitestellidae) had the greatest impact on the variation in community
566 structure. Focusing on these taxa, they appeared to be indicative of different groups,
567 representing different types of microhabitats rather than different sampling locations.
568 In the first group, Spionidae and Terebellida highly contributed to the positioning of
569 the reduced sediments from Cheops and reference samples from Amon. In the
570 second group, Orbitestellidae highly contributed to the positioning of both carbonate
571 crust microhabitats (Pockmark and Amon). Finally Capitellidae and Dorvilleidae
572 presented high contributions in reduced sediments from Amon and Pockmark area
573 (Figure 8a). These three groups were also distinguished on the Ward's cluster
574 (Figure 8b). According to the datasets, the pooling of both carbonate crust
575 microhabitats seemed to be due to their low number of individuals (n=18 and 53)
576 rather than to the presence of shared taxa (Tables 3a, b). When regarding the
577 similarity level defined by the dotted line, the Ward's cluster also showed that the
578 reduced sediments from Cheops had higher similarities with the carbonate crust
579 microhabitats than with the other reduced sediment "soft" microhabitats (Figure 8b).

580

581 A PCA with Hellinger-transformed meiofaunal >250 µm data only (not shown)
582 exhibited the same general distance patterns as the one with macrofauna *sensu*
583 *stricto* (Procruste test stat=0.53, $p=0.013$, 1000 permutations). However, meiofaunal

584 sampling was very incomplete, especially on hard substratum, and these results
 585 might reflect this paucity of observations.

586

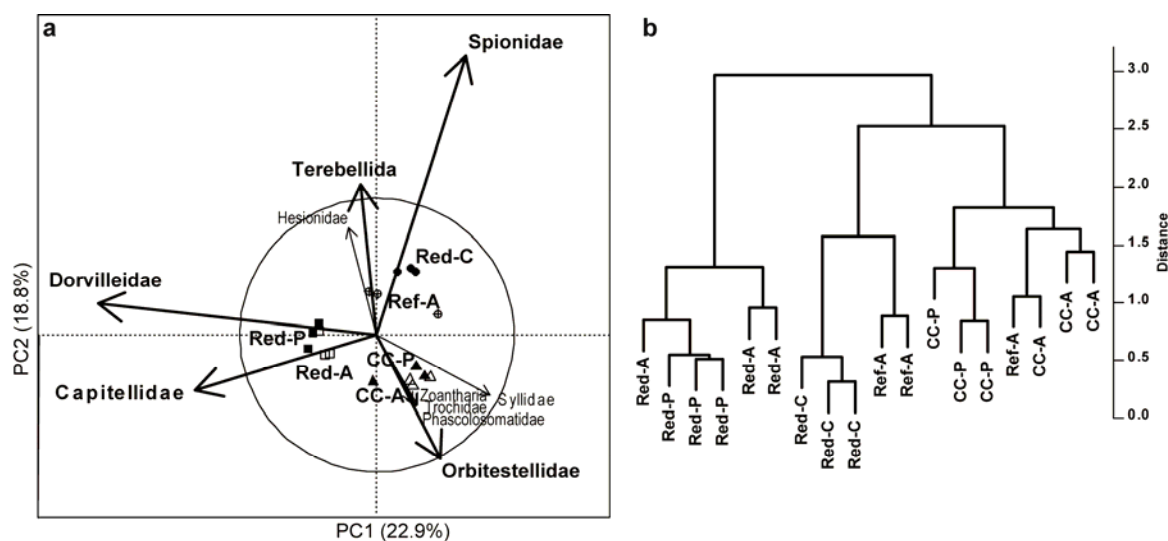


Fig. 8 (a) Principal Component Analysis (PCA, scaling type 1) of Hellinger-transformed macrofaunal abundances on the Amon MV (A), Pockmark area (P) and the Cheops MV (C). The first two axes represent 41.7% of the total variance in macrofaunal abundance. The circle of equilibrium indicates the significant contribution of five taxa (radius=0.65). Vectors shorter than 0.34 were removed. (b) Ward's hierarchical clustering was performed with Hellinger-transformed macrofaunal abundances for each microhabitat types. Red: reduced sediments, CC: carbonate crusts, and Ref: reference sample

587

588

589 4. Discussion

590 This study investigated the differences in faunal diversity in relation to different
 591 habitats and their biogeochemical conditions at three cold seep sites of the NDSF.
 592 Due to inevitably limited submersible time, sampling effort was relatively low given
 593 the high heterogeneity of cold seeps sites. Nevertheless, our results provide the first
 594 insights on seep faunal composition and diversity and their relationships with
 595 environmental conditions in the NDSF area.

596

597 4.1. Difference between the reference site and cold seep habitats at Amon MV

598

599 The reference site did not show any evidence of seepage whether direct (i.e. no
 600 detection of methane and sulphide fluxes) or indirect (i.e. absence of symbiont-
 601 bearing fauna). The fauna found at the reference site was different from that of the
 602 reduced habitats and carbonate crusts from Amon. Densities of macro- and
 603 meiofauna were two-fold lower than in reduced sediments, and total benthic oxygen

604 consumption was an order of magnitude lower. Accordingly, biomass was 1-4 orders
605 of magnitude lower than at all other active sites from Amon. The reference site
606 showed a relatively high evenness, but a lower diversity than the reduced sediment
607 sites of Amon, therefore refuting our initial hypothesis. The reduced sediment
608 microhabitats sampled within the present study support an overall higher faunal
609 diversity compared to close-by oxygenated habitats. This pattern has already been
610 observed on Eel River at about 500 m depth where diversity on clam beds was
611 similar or higher than on non-seep sites (Levin et al. 2003; Levin et al. 2010).
612 However, this is in contradiction with other studies from 770 to 3200 m depth where
613 diversity appears to be lower at active seep sites (Sahling et al. 2002; Levin et al.
614 2010; Menot et al. 2010)

615 Comparing among sites, the relationship between seepage activity and diversity
616 could best explained by a hump-shaped curve. We suggest that at the relatively low
617 sulphide concentrations encountered at Amon the reduced sediments could be
618 considered as an “ecotone” enhancing diversity by presenting a high variability of
619 chemical environment and ecological niches, favoring the establishment of symbiont-
620 bearing fauna but not limiting heterotrophic fauna by toxic concentrations of sulphide
621 (Cordes et al. 2010). In contrast, the Pockmark area or similarly active seeps such
622 as Hydrate ridge (Sahling et al. 2002) appear to show declined diversity, despite the
623 high abundances/biomasses observed, potentially selecting for specialists able to
624 withstand high sulfide concentrations and fluxes.

625

626 4.2. Reduced sediment microhabitats

627 The reduced sediment microhabitats were influenced by fluid emissions as attested
628 by biogeochemical conditions. Sulphide concentrations at 12 cm below the seafloor
629 in the Pockmark area were 10 times higher than what was observed on Amon for the
630 same sediment depth. This flux was associated with a higher oxygen uptake and
631 faster consumption at the water-sediment interface, suggesting higher microbial
632 activity within reduced sediments of the Pockmark area compared to all other sites.
633 According to a previous study (Girnth et al. 2010), some evidences of brine
634 overflowing the sediments were recorded at Amon reduced sediments. However, the
635 homogeneity of the chloride profiles at both sites does not support the presence of
636 upward seepage of saline fluids as observed in some areas of Cheops.

637 Biogeochemical measurements indicate a ranking of activity with the Pockmark
638 reduced sediments as the most sulphidic habitat, followed by Amon and Cheops.

639

640 Accordingly, the reduced sediment microhabitats at Amon and the Pockmark area
641 were colonized by symbiont-bearing species, including siboglinid polychaetes and
642 bivalves (Vesicomidae, Lucinidae, Mytilidae and Thyasiridae) as well as by dorvilleid
643 and capitellid polychaetes. The presence of these two families provides direct
644 evidence for fluid emissions as they are usually associated with areas rich in organic
645 matter and with sulphidic environments (Rouse and Fauchald 1997). Dorvilleid
646 polychaetes also dominate reduced sediment microhabitats from other seep sites at
647 1100 m depth in the Marmara Sea (Ritt et al. 2010), at 2020 m depth in the
648 Mediterranean Sea (Amsterdam MV, Ritt et al., in prep.) and at 500 m depth at the
649 Eel River off California (Levin et al. 2003). Large nematodes were abundant in the
650 reduced sediments of Amon, as previously observed on other mud volcanoes at 1220
651 (Van Gaever et al. 2006) and 5000 m depth (Olu et al. 1997).

652

653 The fauna in the reduced sediment microhabitat from Amon hosted the highest
654 abundance of symbiont-bearing species, and its macrofaunal taxonomic richness
655 was two times higher than in the Pockmark area. The bivalve species observed in the
656 Pockmark area either harbored sulphide-oxidizing endosymbionts such as *Lucinoma*
657 *kazani* and *Isorropodon perplexum* (Salas and Woodside 2002; Olu-Le Roy et al.
658 2004) or different types of symbionts as in the undetermined species *Idas sp.* Med,
659 (Duperron et al. 2008).

660

661 On Cheops, the reduced sediments sampled were located about 250 m away from a
662 brine lake which features extreme physico-chemical conditions. Methane
663 concentrations at the surface of the lake varied from 2.4 to 3.7 mmol l⁻¹ with
664 temperatures of 20-40°C and salinities 210 to 244 g l⁻¹ (Mastalerz, Harmegnies, pers.
665 com.). Sediment cores revealed a dark layer covering a layer of brown hemipelagic
666 sediments, suggesting the occurrence of a relatively recent sulphidic mud flow.
667 Sulfate reduction rates and oxygen consumption rates were considerably lower than
668 at the other sites, indicating a low sulphide flux, as confirmed by pore water
669 measurements. Accordingly, despite the detection of elevated methane
670 concentrations in the bottom waters of Cheops above the reduced sediments, no

671 symbiont-bearing fauna was observed. This microhabitat was dominated by spionid
672 (~2200 individuals m⁻²) or terebellid (~660 individuals m⁻²) polychaetes, commonly
673 found in sandy or muddy environments, from intertidal habitats to abyssal depths
674 (Rouse and Pleijel 2001). Dense Terebellida beds, especially the Ampharetidae
675 family have been observed at about 1100 m depth on the New Zealand margin
676 (Sommer et al. 2009) and in the Marmara Sea (Ritt et al. 2010), as well as at 770 m
677 at Hydrate Ridge off Oregon (Levin et al. 2010) where methane concentrations in the
678 bottom water reach up to 2 mmol l⁻¹ and 0.7 μmol l⁻¹, respectively for the first two first.
679 At Cheops, methane concentrations varied between 4 and 8 μmol l⁻¹. This suggests
680 that terebellids are able to inhabit a wide range of environmental conditions. Further
681 chemical measurements are needed to have a better understanding of the intriguing
682 processes occurring within reduced sediments on Cheops.

683

684 4.3. Carbonate crust microhabitats

685 As expected, the difference in substratum between the soft sediment and carbonate
686 crust microhabitats appears to influence the composition and distribution of the seep
687 fauna in the NDSF. Nevertheless, the clustering of the CC microhabitats from Amon
688 and the Pockmark area appears to be due to the low number of sampled individuals
689 rather than the presence of common taxa. Sampling efficiency on hard substrata
690 does not appear to be ideal as suggested by the high heterogeneity between
691 replicates and the low Jaccard's similarity coefficients obtained. However these
692 results may reflect the real heterogeneity of this habitat in terms of faunal
693 composition and spatial distribution. Visual observations showed that the carbonate
694 crusts sampled in the Pockmark area were associated with reduced sediments
695 whereas those from Amon did not appear to be located in the vicinity of an active
696 area. In addition, the crusts showed different facies and colour that may reflect
697 different fluid intensities and stages of evolution (Bayon et al. 2009a). For example,
698 the carbonates from the south-western part of Amon are thick, dark and cemented,
699 and can reach 1 m of thickness. They may have been formed in the distant past,
700 during a period of intense fluid emissions (Dupré et al. 2007). The absence of
701 symbiont-bearing fauna and the dark color of crusts — due to their exposure to
702 oxygen-rich bottom water and their iron and manganese oxide cover — corroborate
703 the hypothesis that these carbonates may be relatively old. Fluid emissions may be
704 very low on this part of Amon, explaining the absence of symbiont-bearing fauna. The

705 low faunal densities and biomass further support the fact that this environment is not
706 favorable, neither to symbiont-bearing fauna, nor to heterotrophic fauna.

707

708 The light-colored and crumbly carbonates from the Pockmark area differed
709 morphologically from the “inactive” crusts found on Amon as they seem to be
710 relatively young. The precipitation of authigenic carbonates is controlled by high
711 alkalinity of pore waters (Aloisi et al. 2002; Michaelis et al. 2002) due to the activity of
712 consortia of archaea and bacteria involved in the anaerobic oxidation of methane
713 (AOM) coupled to sulphate reduction (Boetius et al. 2000). Another by-product of
714 AOM is sulphide which may support sulphide-oxidizing symbionts of chemosynthetic
715 fauna such as the siboglinid polychaetes found beneath the crusts. In addition, the
716 methane concentrations were high, reaching $>5 \mu\text{mol l}^{-1}$. Siboglinids may contribute
717 to bio-irrigation and favor advection and diffusion processes that play a significant
718 role in carbonate precipitation (Bayon et al. 2009a).

719

720 4.4. Comparison between Amon, the Pockmark area and Cheops

721 The reduced sediment microhabitats appeared to be distributed along a gradient
722 related to seepage intensity and thus, to methane, oxygen and sulphide fluxes; with
723 the Pockmark area as the most intense seepage site. The fauna from the reduced
724 sediment microhabitats of the Pockmark area and Amon were rather similar and
725 highly influenced by the presence of symbiotic organisms as well as dorvilleid and
726 capitellid polychaetes, usually associated with organically enriched, reduced
727 environments (Rouse and Pleijel 2001). Both communities showed relatively similar
728 oxygen consumption rates. The taxonomic diversity was higher on Amon followed by
729 the Pockmark area and Cheops. However, the reduced sediments, associated with
730 the debris-flow of the Pockmark area, were more sulphidic and probably also more
731 stable than the fresh Amon mud flow. The lower diversity and biomass observed in
732 the reduced sediments of the Pockmark could be due to the high level of sulphide
733 flux limiting the survival of most benthic species.

734

735 At the time of sampling, the mud flow at Cheops was probably recent as only a very
736 thin sulphidic horizon was observed on top of hemipelagic sediments. These
737 conditions may explain the lower diversity and the lack of symbiont-bearing fauna on
738 the sampling site located 250 m away from the central brine lake. According to video

739 observations, instability seems to decrease from the summit toward the periphery as
740 suggested by the presence of carbonate crusts with symbiont-bearing mytilids at
741 about 700 m away from the lake.

742

743 4.5. Comparison at a larger scale

744 In terms of seepage activity, Amon is comparable to the Håkon Mosby MV (1200 m
745 depth) from the Norwegian margin and the Amsterdam MV (2020 m depth) located
746 on the Mediterranean Ridge. These MVs discharge mud, fluids and gases from their
747 summits, which undergo episodic mud eruptions (Zitter et al. 2005; Dupré et al. 2007;
748 Feseker et al. 2008). This activity induces instability and chemical gradients that
749 influence the distribution of fauna, which is concentrically distributed around a chaotic
750 summit (Zitter et al. 2005; Jerosch et al. 2007). The reduced site sampled at Amon
751 was located on the base of the mud volcano, and influenced by lateral brine and mud
752 flows (Girnth et al. 2011). Interestingly, the dimensions of the reduced sediment site
753 was rather small (ca. 250 m) and the next larger reduced sediment patches were >2
754 km away.

755

756 The carbonate crusts and reduced sediments of the Pockmark area from the NDSF
757 showed similarities with a more recently discovered site, the giant REGAB pockmark
758 in the Gulf of Guinea at 3160 m depth. There, carbonate crusts are colonized by
759 dense mussel beds and siboglinid assemblages (Olu-Le Roy et al. 2007). Pockmark
760 and carbonate crust areas have also been observed at 740 m depth on the Storegga
761 slide and the Nyegga area located on the north-west of the Norway margin which
762 have undergone slide events. There, benthic fauna is represented by Siboglinidae,
763 Crinoidea, Pycnogonidae and microbial mats (Hovland et al. 2005; Hovland and
764 Svensen 2006; Paull et al. 2008). However, these features are taller than those
765 observed in the central province of the NDSF as they reach 190 m long and 40 m
766 wide, while pockmarks do not exceed a few meters in diameter at the NDSF study
767 site.

768

769 The Cheops MV share similarities with the Napoli MV located on the Mediterranean
770 Ridge at 1900 m depth, as they both harbor brine seepages (Charlou et al. 2003).
771 However, faunal density and taxonomic richness on Cheops are lower than those
772 observed on Napoli (Ritt et al., in prep). Faunal composition and distribution may be

773 strongly linked to the activity of the MV. Mud flows may initiate higher sedimentary
774 and chemical instabilities on Cheops, limiting the colonization of benthic species.
775 Although considered as an extreme habitat, the vicinity of brine lakes can be
776 colonized by dense colonies of Porifera as observed on Napoli (Ritt, pers obs) or by
777 dense mussel communities, such as those found on the shoreline of brine pools in
778 the Gulf of Mexico at 650 m depth (Macdonald et al. 1990; Smith et al. 2000). The
779 absence of dense assemblages of symbiont-bearing fauna close to the brines on
780 Cheops was thus unexpected and may be explained by the effect of recent
781 disturbances.

782

783 In conclusion, our comparative investigation of active cold seeps on the NDSF
784 suggested that seepage activity substantially enhanced benthic activity, biomass and
785 diversity compared to the surrounding oxygenated and oligotrophic deep-sea
786 environments. The biomass and biogeochemical activity of seep associated
787 communities is 1-2 orders of magnitude higher than the surrounding and diversity
788 was increased by a factor of 1.5. Reduced sediment microhabitats exhibited highest
789 biomasses and diversity in comparison with surrounding oxygenated areas
790 (reference site). As expected, reduced sediments and carbonate crusts were
791 characterized by distinct faunal composition and faunal similarities were observed
792 within each microhabitat type regardless of the site and geological structure (i.e. mud
793 volcano, pockmark). However, our heterogeneous results on carbonate crusts require
794 more investigation and emphasize the importance of developing a specific sampling
795 tool dedicated to hard substratum in the deep sea. No simple relationship was
796 detected between chemical conditions, sediment instability, fluid intensity and
797 community structure although there seems to be a gradient related to seepage
798 intensity between the different sites (Pockmark>Amon>Cheops). Further
799 investigations with an appropriate sampling strategy, especially regarding the
800 meiofauna, may help in highlighting the links between faunal distribution and
801 environmental conditions in the NDSF. Most likely, temporal dynamics in such active
802 geological systems may be very important in structuring community diversity. It could
803 be studied in the future by deploying autonomous video cameras and sensors as well
804 as by regularly monitoring a same site. Time-series data would help determine the
805 response of the fauna to instabilities and disturbances induced by the occurrence of

806 mud flows or brine seepage, and in which ways local diversity is related to temporal
807 fluctuations and stability of habitats.

808

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830

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Table 1. Location, depth, and tools used to perform physico-chemical and faunal sampling at each microhabitat from the different sampling sites of the Nile Deep-Sea Fan explored during the BIONIL (2006) and MEDECO (2007) cruises. Sampling effort, length of each sediment cores and estimated surface of each piece of carbonate crusts are also reported. Further details of samples are archived in <http://www.pangaea.de/PHP/CruiseReports.php?b=HERMES>

Microhabitat types	Latitude (°N)	Longitude (°E)	Depth (m)	Physico-chemical measurements	Faunal sampling
Reference site [ca. 15 km away from Amon MV (BIONIL, 2006)]					
Reference site (Ref)	32°21.42'	31°32.50'	1000	3 tubes (multicorer) M70/2b_785	3 tubes (74 cm ² each) Ref1 (20 cm) Ref2 (20 cm) Ref3 (20 cm)
Eastern Province – Amon MV (BIONIL, 2006)					
Reduced sediments (Red)	32°22.05'	31°42.27'	1154	Microsensor , chamber and porewater samples PC15, 46, 47 M70/2b_765 (D115) M70/2b_790 (D121)	3 blade cores (200 cm ² each) Red1 (BCROV-2, 10 cm) Red2 (BCROV-3, 10 cm) Red3 (BCROV-8, 10 cm)
Carbonate crusts (CC)	32°22.05'	31°42.27'	1153	None	3 pieces of crust CC1 (SFS-11, 84 cm ²) CC2 (SFS-111, 103 cm ²) CC3 (SFS-2, 139 cm ²)
Central Province – Pockmark area, site 2A (BIONIL 2006)					
Reduced sediments (Red)	32°32.01'	30°21.13'	1697	Microsensor, chamber and porewater samples PC9, 52 M70/2b_784 (D120) M70/2b_841 (D127)	3 blade cores (200 cm ² each) Red1 (BCROV-3, 20 cm) Red2 (BCROV-7, 17 cm) Red3 (BCROV-8, 20 cm)
Carbonate crusts (CC)	32°32.00'	30°21.18'	1696	None	3 pieces of crust CC1 (SFS-5, 48 cm ²) CC2 (SFS-7, 81 cm ²) CC3 (SFS-8, 34 cm ²)
Western Province – Cheops MV (MEDECO, 2007)					
Reduced sediments (Red)	32°08.05'	28°09.67'	3007	3x2 water samples: CH ₄ MEDECO2_D343-PEPITO A-1 and PEPITO A-2, A-2, B-1, B-2, C-1 and C-2	3 blade cores (200 cm ² each) Red1 (BL-2, 20 cm) Red2 (BL-4, 19 cm) Red3 (BL-6, 17 cm)

Table 2. Physico-chemical characterization of the bottom water environment at the three study areas. Only the methane data from the Cheops MV were obtained directly above the organisms in this study. Amon data were provided by Girnth et al. (2011), Pockmark data by Grünke et al. (in press). ΣS = Total dissolved sulphides ($H_2S+HS^-+S^{2-}$), SR = Sulphate reduction rate. The reference site was ca. 15 km away from the active centre of the Amon MV.

	pH	[O ₂] Bottom water ($\mu\text{mol l}^{-1}$)	[O ₂] Penetration depth (cm)	[O ₂] Total benthic consumption ($\text{mmol m}^{-2} \text{d}^{-1}$)	[SO ₄ ²⁻] Porewater (mmol l^{-1})	[Cl ⁻] Porewater (mmol l^{-1})	[CH ₄] Bottom water ($\mu\text{mol l}^{-1}$)	[ΣS] Porewater (mmol l^{-1})	[ΣS] Porewater top 5 cm/peak conc. (mmol l^{-1})	SR Sediments ($\text{mmol m}^{-2} \text{d}^{-1}$)
Amon MV										
Reference site (Ref)	8.20 ^a	230 ^a	>4 ^a	< 1 ^a	31.4 ^a	529 ^a	0.0 ^a	0 ^a	-	< 0.2 ^a
Reduced sediments (Red)	7.88 ^b	150-200 ^b	0.0-0.25 ^b	10-46 ^c	30.7-40.3 ^d	404-580 ^d	0.0 ^d	< 0.7 ^b	0.8/2.5 ^d	0.5 ± 0.2 (n=3) ^d
Pockmark area										
Reduced sediments (Red)	8.11 ^b	230 ^e	0.1-0.2 ^b	156-174 ^c	29.1-29.8 ^d	606-630 ^d	0.2-0.3 ^e	0.2 ^b 0.7 ^d	0.8/25 ^d	22-41 ^d
Cheops MV										
Reduced sediments (Red)	-	220 ^e	-	111-130 ^c	-	-	3.60-9.34 ^f	-	-	5-14 ^d

Devices used to acquire the data: (a) multicorer, (b) microprofiler, (c) benthic chamber, (d) PCs, (e) KIPS bottle, (f) PEPITO, (-) no available data

Table 3. AMON - Macrofaunal (>250 µm) densities (individuals m⁻²) per replicate and relative abundance (%) of each taxa in the microhabitats studied on the Amon mud volcano: reduced sediments (Red, n=3), carbonate crusts (CC, n=3) and the reference site (Ref, n=3). Total densities and relative abundances from each taxonomic group are highlighted in bold. Und. = undetermined individuals. (*) Taxonomic level used for alpha-diversity analyses, here mostly family level. All sampling was performed during the BIONIL cruise (2006).

Taxonomic groups	Reduced sediments				Carbonate crusts				Reference samples			
	Red1	Red2	Red3	%	CC1	CC2	CC3	%	Ref1	Ref2	Ref3	%
Cnidaria (Total)	0	0	0	0	0	0	935	72.21	0	270	135	17.65
Anthozoa – Zoantharia*	0	0	0	0	0	0	935	72.21	0	0	0	0
Medusozoa – Scyphozoa*	0	0	0	0	0	0	0	0	0	270	135	17.65
Polychaeta (Total)	1900	400	1650	82.29	119	0	144	16.67	541	405	676	70.59
Capitellidae*	1100	100	50	26.04	0	0	0	0	0	0	0	0
Dorvilleidae*	300	50	1250	33.33	0	0	0	0	135	135	0	11.76
Hesionidae*	0	0	50	1.04	0	0	0	0	0	0	0	0
Paraonidae*	0	0	0	0	0	0	0	0	135	0	0	5.88
Pholoidae*	0	0	0	0	0	0	144	11.11	0	0	0	0
Phyllodocidae*	100	0	0	2.08	0	0	0	0	0	0	0	0
Spionidae*	100	0	50	3.13	0	0	0	0	135	135	405	29.41
Siboglinidae, Frenulata*	300	50	200	11.46	0	0	0	0	0	0	0	0
Syllidae*	0	0	0	0	119	0	0	5.56	0	0	270	11.76
Terebellida*	0	150	50	4.17	0	0	0	0	135	135	0	11.76
Larvae	0	50	0	1.04	0	0	0	0	0	0	0	0
Bivalvia (Total)	100	150	300	11.46	0	0	0	0	0	0	0	0
Lucinidae*												
<i>Lucinoma kazani</i>	0	150	50	4.17	0	0	0	0	0	0	0	0
Mytilidae*												
<i>Idas modiolaeformis</i>	50	0	0	1.04	0	0	0	0	0	0	0	0
Thyasiridae*												
<i>Thyasira striata</i>	0	0	100	2.08	0	0	0	0	0	0	0	0
Vesicomysidae*												
<i>Isorropodon perplexum</i>	0	0	150	3.13	0	0	0	0	0	0	0	0
Sareptidae*												
Und. Sareptidae	50	0	0	1.04	0	0	0	0	0	0	0	0
Gastropoda (Total)	0	50	0	1.04	0	0	72	5.56	0	0	0	0
Calliotropidae*												
<i>Putzeysia wiseri</i>	0	0	0	0	0	0	72	5.56	0	0	0	0
Und. Gastropoda*	0	50	0	1.04	0	0	0	0	0	0	0	0
Sipuncula (Total)	0	0	0	0	0	97	0	5.56	0	0	135	5.88
Phascolosomatidae*												
<i>Phascolosoma aff. granulatum</i>	0	0	0	0	0	97	0	5.56	0	0	0	0
Golfingiidae*												
<i>Nephasoma minutum</i>	0	0	0	0	0	0	0	0	0	0	135	5.88
Crustacea (Total)	50	50	150	5.21	0	0	0	0	0	0	135	5.88
Decapoda-Thalassinidae*	0	0	50	1.04	0	0	0	0	0	0	0	0
Cumacea- Nannastacidae*												
<i>Cumella pygmaea</i>	0	0	50	1.04	0	0	0	0	0	0	0	0
Isopoda*	0	0	0	0	0	0	0	0	0	0	135	5.88
Leptostraca*	50	0	0	1.04	0	0	0	0	0	0	0	0

Larvae	0	50	50	2.09	0	0	0	0	0	0	0	0
Total density (ind. m⁻²)	2050	650	2100		119	97	1151		541	676	1081	

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Table 4. POCKMARK area and CHEOPS - Macrofaunal (>250 µm) densities (individuals m⁻²) per replicate and relative abundance (%) of each taxa in the microhabitats studied in the Pockmark area: reduced sediments (Red, n=3), carbonate crusts (CC, n=3) and on the Cheops MV: reduced sediments (Red, n=3). Total densities and relative abundances from each taxonomic group are highlighted in bold. Und. = undetermined individuals. (*) Taxonomic level used for alpha-diversity analyses, here mostly family level. All sampling was performed during the BIONIL (2006) and MEDECO (2007) cruises.

Taxonomic groups	Pockmark area								Cheops MV			
	Reduced sediments				Carbonate crusts				Reduced sediments			
	Red1	Red2	Red3	%	CC1	CC2	CC3	%	Red1	Red2	Red3	%
Polychaeta (Total)	2550	2650	1800	83.83	1042	123	4412	39.62	3800	5100	3000	95.58
Capitellidae*	450	650	250	16.16	208	0	0	1.89	0	0	0	0
Cirratulidae*	0	0	0	0	208	0	0	1.89	0	0	0	0
Dorvilleidae*	1350	1500	1350	50.30	208	0	0	1.89	0	0	50	0.40
Glyceridae*	50	0	0	0.60	0	0	0	0	0	0	0	0
Hesionidae*	500	350	200	12.57	417	0	588	7.55	950	1050	1050	24.50
Sabellidae*	0	0	0	0	0	0	2941	18.87	0	0	0	0
Spionidae*	100	100	0	2.40	0	123	0	1.89	2750	2750	1300	54.62
Syllidae*	0	0	0	0	0	0	294	1.89	0	0	0	0
Terebellida*	100	50	0	1.80	0	0	588	3.77	100	1300	600	16.06
Bivalvia (Total)	350	500	50	10.78	0	0	1176	7.55	0	0	0	0
Lucinidae*												
<i>Lucinoma kazani</i>	0	100	0	1.20	0	0	0	0	0	0	0	0
Und. Lucinidae	0	100	0	1.20	0	0	0	0	0	0	0	0
Mytilidae*												
<i>Idas modiolaeformis</i>	0	0	0	0	0	0	1176	7.55	0	0	0	0
Vesicomyidae*												
<i>Isorropodon perplexum</i>	100	150	0	2.99	0	0	0	0	0	0	0	0
Und. Bivalvia	150	150	50	5.39	0	0	0	0	0	0	0	0
Gastropoda (Total)	0	350	100	5.39	1667	1728	1471	50.94	0	50	50	0.80
Calliotropidae*												
<i>Putzeysia wiseri</i>	0	0	0	0	208	123	294	5.66	0	0	0	0
Trochidae*	0	0	0	0	208	123	588	7.54	0	0	0	0
Skeneidae*												
<i>Akritogyra conspicua</i>	0	0	0	0	0	123	0	1.9	0	0	0	0
Und. Skeneidae	0	100	0	1.20	0	0	0	0	0	0	0	0
Orbitestellidae*												
<i>Lurifax vitreus</i>	0	0	0	0	1250	1358	588	35.85	0	0	0	0
Und. Gastropoda	0	250	100	4.19	0	0	0	0	0	50	50	0.80
Crustacea (Total)	0	0	0	0	0	0	294	1.89	200	100	150	3.61
Amphipoda-Gammaridae												
Sebidae*												
<i>Seba sp.</i>	0	0	0	0	0	0	294	1.89	0	0	0	0
Und. Gammaridae	0	0	0	0	0	0	0	0	50	0	0	0.40
Leptostraca												
Nebaliidae*	0	0	0	0	0	0	0	0	0	0	50	0.40
Und. Leptostraca	0	0	0	0	0	0	0	0	150	100	100	2.81
Total density (ind. m⁻²)	2900	3500	1950		2708	1852	7353		4000	5250	3200	

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Table 5. AMON - Meiofaunal (>250 µm) densities (individuals m⁻²) per replicate and relative abundance (%) of each taxa in the reduced sediment microhabitat (Red, n=3) studied on the Amon and in the reference samples (Ref, n=3). Total densities and relative abundances from each taxonomic group are highlighted in bold. Und. = undetermined individuals. (*) Taxonomic level used for alpha-diversity analyses, here mostly family level. All sampling was performed during the BIONIL cruise (2006).

Taxonomic groups	Reduced sediments				Carbonate crusts				Reference site			
	Red1	Red2	Red3	%	CC1	CC2	CC3	%	Ref1	Ref2	Ref3	%
Nematoda (Total)	74650	29900	28300	95.15	0	388	0	100	405	135	405	77.78
Crustacea (Total)	900	1900	4000	4.85	0	0	0	0	270	0	0	22.22
Copepoda-Harpacticoida												
Miraciidae*												
<i>Bulbamphiascus imus</i>	500	1050	200	1.24	0	0	0	0	0	0	0	0
<i>Bulbamphiascus</i> sp.1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Thyphlamphiascus confusus</i>	0	0	550	0.39	0	0	0	0	0	0	0	0
Ameiridae*												
<i>Amphiascus</i> sp.2	0	0	0	0	0	0	0	0	0	0	0	0
<i>Haifameira archibenthoica</i>	0	400	2400	2.00	0	0	0	0	0	0	0	0
<i>Haifameira</i> sp.1	0	0	200	0.14					0	0	0	0
Agestidae*												
<i>Eurycletodes</i> sp.	0	0	0	0	0	0	0	0	270	0	0	22.22
Tisbidae*												
<i>Tisbella</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0
Und. Harpacticoida	0	0	50	0.07	0	0	0	0	0	0	0	0
Copepoda-Cyclopoida												
Oncaeidae*												
<i>Oncaea</i> sp.	0	0	50	0.04	0	0	0	0	0	0	0	0
Copepoda-Calanoidea*												
<i>Calanoidea</i> sp.1	0	150	450	0.43	0	0	0	0	0	0	0	0
<i>Calanoidea</i> sp.	0	300	0	0.21	0	0	0	0	0	0	0	0
Und. Calanoidea	300	0	0	0.21	0	0	0	0	0	0	0	0
Ostracoda												
Polycopidae*												
<i>Polycope</i> sp.3M	50	0	0	0.04	0	0	0	0	0	0	0	0
Pontocyprididae*												
<i>Propontocypris</i> sp.2M	0	0	1	0.04	0	0	0	0	0	0	0	0
<i>Propontocypris</i> cf. <i>levis</i>	50	0	0	0.04	0	0	0	0	0	0	0	0
% Meiofauna / Total fauna	97.36	98.30	93.71		0	80.00	0		55.56	16.67	27.27	
Total density (ind. m⁻²)	75500	31800	32300		0	388	0		676	135	405	

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Table 6. POCKMARK area and CHEOPS – Meiofaunal (>250 µm) densities (individuals m⁻²) per replicate and relative abundance (%) of each taxa in the microhabitats studied on the Pockmark area: reduced sediments (Red, n=3), carbonate crusts (CC, n=3) and on the Cheops mud volcano (MV): reduced sediments (Red, n=3). Total densities and relative abundances from each taxonomic group are given in bold. Und. = undetermined individuals. (*) Taxonomic level used for alpha-diversity analyses, here mostly family level. All sampling was performed during the BIONIL (2006) and MEDECO (2007) cruises.

Taxonomic groups	Pockmark area								Cheops MV			
	Reduced sediments				Carbonate crusts				Reduced sediments			
	Red1	Red2	Red3	%	CC1	CC2	CC3	%	Red1	Red2	Red3	%
Nematoda (Total)	1100	500	1000	36.11	5417	247	2941	97.44	750	2850	600	100
Crustacea (Total)	2850	1300	450	63.89	0	123	0	2.56	0	0	0	0
Copepoda-Harpacticoida												
Miraciiidae*												
<i>Bulbamphiascus imus</i>	1450	850	350	36.81	0	0	0	0	0	0	0	0
Ameiridae*												
<i>Amphiascus sp.2</i>	0	0	0	0	0	123	0	2.56	0	0	0	0
Tisbidae*												
<i>Tisbella sp.</i>	50	0	0	0.69	0	0	0	0	0	0	0	0
Copepoda-Cyclopoida												
<i>Cyclopina sp.</i>	0	250	0	3.47								
Copepoda-Calaonida*												
<i>Calanoida sp.1</i>	100	0	0	1.39	0	0	0	0	0	0	0	0
<i>Calaonida sp.2</i>	50	0	0	0.69	0	0	0	0	0	0	0	0
<i>Calaonida sp.3</i>	50	0	0	0.69	0	0	0	0	0	0	0	0
<i>Calanoida sp.</i>	250	0	0	3.47	0	0	0	0	0	0	0	0
Ostracoda												
Pontocyprididae*												
<i>Propontocypris sp.1M</i>	50	0	0	0.69	0	0	0	0	0	0	0	0
<i>Propontocypris cf. levis</i>	700	200	100	13.89	0	0	0	0	0	0	0	0
<i>Propontocypris cf. setosa</i>	50	0	0	0.69	0	0	0	0	0	0	0	0
<i>Argilloecia sp.</i>	50	0	0	0.69	0	0	0	0	0	0	0	0
Chelicerata												
Und. Acarina*	50	0	0	0.69	0	0	0	0	0	0	0	0
% Meiofauna / Total fauna	57.66	33.96	42.65		66.67	16.67	28.57		15.79	35.19	15.79	
Total density (ind. m⁻²)	3950	1800	1450		5417	370	2941		750	2850	600	

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Table 7. RED - Biological descriptors of the reduced sediment microhabitats sampled on the Amon MV, the Pockmark area and the Cheops MV in the Nile Deep-Sea Fan. The highest values are highlighted in bold. The meiofaunal data includes only the large meiofauna >250 µm. The number equivalent of Shannon and Simpson indices are given in italics

Biological descriptors	Amon	Pockmark area	Cheops
Macrofauna -dominant	Polychaetes reaching 82.3% of total abundance (Dorvilleidae, Capitellidae)	Polychaetes reaching 83.8% of total abundance (Dorvilleidae)	Polychaetes, reaching 95.6% of total abundance (Spionidae, Hesionidae)
Macrofauna -others	Bivalves, crustaceans, gastropods	Bivalves, gastropods	Crustaceans, gastropods
Mean macrofaunal densities (individuals m ⁻²)	1 600 ± 912	2 783 ± 782	4 150 ± 1 033
Mean Jaccard's similarity	0.32	0.47	0.77
Symbiont-bearing fauna	17.1 – 36.4%	0 - 10%	0%
Total macrofaunal biomass (kg preserved wet weight m ⁻²)	1.2*10⁻¹ ± 1*10⁻¹	1.2*10 ⁻³ ± 1*10 ⁻³	6.4*10 ⁻³ ± 3*10 ⁻³
Macrofaunal diversity indices			
Total richness (S)	15	9	6
Shannon (H _e [']) <i>Exp (H_e['])</i>	1.93 6.89	1.35 3.86	1.05 2.86
Gini-Simpson (D _{GS}) <i>(1 / 1-D_{GS})</i>	0.78 4.62	0.63 2.68	0.59 2.44
Evenness (J')	0.71	0.61	0.59
Meiofauna (>250µm) -dominant	Nematodes with 95.2% of the total abundance	Copepods with 63.9% of the total abundance	100% nematodes
Meiofauna (>250µm) -others	Copepods, ostracods (6%)	Acarina (1.3%)	-
Mean meiofaunal densities (individuals m ⁻²)	46 733 ± 25 004	2 400 ± 1 354	1 400 ± 1258
Mean Jaccard's similarity	0.31	0.41	0.67
Meiofaunal diversity indices			
Total richness (S)*	7	7	1
Nematoda richness	1	1	1
Copepoda richness	4	3	0
Ostracoda richness	2	2	0
Acarina richness	0	1	0
Shannon (H _e [']) <i>Exp (H_e['])</i>	0.24 1.27	1.39 4.01	0
Gini-Simpson (D _{GS}) <i>(1 / 1-D_{GS})</i>	0.09 1.10	0.70 3.37	-
Evenness (J')	0.12	0.71	-

Table 8. CC and Ref - Biological descriptors of the carbonate crust microhabitats sampled on the Amon MV, in the Pockmark area and at the reference site (Amon MV) in the Nile Deep-Sea Fan. The highest values are highlighted in bold. The meiofauna data includes only the large meiofauna >250 µm. The number equivalent of Shannon and Simpson indices are given in italics

Biological descriptors	Carbonate crusts		Reference site
	Amon	Pockmark area	Amon
Macrofauna -dominant	Cnidarians (Zoantharia) reaching 72.2% of total abundance	Gastropoda (<i>Lurifax vitreus</i>) and polychaetes (Sabellidae) in various proportions, reaching 50.9, 39.6% of total abundance	Polychaetes, reaching a mean of 70.6% of total abundance (Spionidae)
Macrofauna -others	Gastropods, sipunculians	Bivalves, crustaceans	Cnidarians, sipunculians, crustaceans
Mean macrofaunal densities (individuals m ⁻²)	456 ± 602	3 971 ± 2 960	766 ± 281
Mean Jaccard's similarity	0.0	0.31	0.34
Symbiont-bearing fauna	0%	0 -16%	0%
Total macrofaunal biomass (kg preserved wet weight m ⁻²)	1.8*10 ⁻³ ± 5*10 ⁻²	3*10⁻² ± 5*10⁻²	3.2*10 ⁻⁵ ± 6*10 ⁻⁵
Macrofaunal diversity indexes			
Total richness (S)	5	14	8
Shannon (H _e [']) <i>Exp (H_e['])</i>	0.96 2.61	2.08 8.00	1.92 6.82
Gini-Simpson (D _{GS} = 1 - λ) (1 / λ)	0.46 1.84	0.81 5.31	0.83 5.90
Evenness (J')	0.60	0.79	0.92
Meiofauna (>250µm) -dominant	Only 4 individuals (nematodes)	Nematodes with 97.4% of the total abundance	Only 9 individuals (nematodes, copepods)
Meiofauna (>250µm)-others	-	Copepods (11%)	-
Mean meiofaunal densities (individuals m ⁻²)	129 ± 224	2 909 ± 2 523	-
Mean Jaccard's similarity	-	0.67	-
Meiofaunal diversity indexes			
Total richness (S)*	1	2	2
Nematoda richness	1	1	1
Copepoda richness	0	1	1
Ostracoda richness	0	0	0
Shannon (H _e [']) <i>Exp (H_e['])</i>	-	0.12 1.13	-
Gini-Simpson (D _{GS} = 1 - λ) (1 / λ)	-	0.05 1.05	-

Evenness (J')

-

0.17

-

90
91
92
93
94
95