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The benthic fauna of slope pockmarks from the Kostarrenkala area (Capbreton canyon, SE Bay of Biscay)

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Abstract

Numerous slope pockmarks were recently discovered by multibeam mapping in the Kostarrenkala area. The benthic and suprabenthic communities of some of 3 of these pockmarks were sampled for the first time, using a box corer and a sledge. All the species collected during this survey have been previously found elsewhere in surrounding non-pockmark areas. Except for a single thyasirid bivalve (only 1 specimen sampled), none of them are known to host symbiotic bacteria and inhabit seeping environments. The apparent absence of fluid emission in the water column, the lack of carbonate concretions at the bottom of these depressions, and the similarity in faunal composition of adjacent slope benthic communities combine to suggest that the 3 pockmarks investigated during this survey should be considered inactive fossil depressions. However, such a conclusion cannot be extended to the area's deeper pockmarks, where near-bottom turbid waters have been detected from video recordings. Therefore, further investigations need to be carried out on these deep depressions for a better understanding of their actual seeping activity.

• **Key words:** Pockmarks, benthic communities, NE Atlantic Ocean, Bay of Biscay, Kostarrenkala fishing ground.

Laburpena

Ezpondako *pockmark* ugari aurkitu berri dira Kostarrenkala inguruetan sorta anitzeko kartografiaz (*multibeam mapping*). Horietako hiru pockmarketan komunitate bentiko eta suprabentikoen laginak hartu dira lehen aldiz, *box corer* eta lera erabiliz. Ikerketa honetan jaso diren espezie guztiak lehendik ere pockmark inguruak ez diren hurbileko zonetan aurkituak izan dira. Thyasiridae familiako bibalbio espezie bat izan ezik (ale bakar bat jaso zen), gainontzeko espezieetatik bat bera ere ez da ezagutzen bakterio

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sinbiotiko ostalaririk dituenik, ezta emanazio hotzeko inguruetan (*seeping environment*) bizi denik ere. Itxura batean ur zutabean fluido emisio nabarmenik ez egoteak, sakonune hauen hondoan karbonato konkreziorik ez egoteak, eta komunitate faunistikoa inguruko ezpondako komunitate bentoniko antzekoa izateak, ikertu diren hiru *pockmark* hauek sakonune fosil ez aktibotzat hartzea iradokitzen dute. Halere, halako ondoriorik ezin zaie aplikatu ikertu den zonaldean sakonera handiagoetan aurkitzen diren beste *pockmark*eri, non hondotik hurbileko ur-uherrak detektatu baitira bideo irudietan. Ondorioz, beharrezkoa litzateke sakoneko sakonune hauetan ikerketa gehiago egitea, gaur egun duten iragazketa aktibitatea hobeto ulertu nahi bada.

• GAKO-HITZAK: *Pockmark*, komunitate bentikoak, IE Ozeano Atlantikoa, Bizkaiko Golkoa, Kostarrenkala arrantza lekua.

RESUMEN

Numerosos *pockmarks* de talud han sido recientemente descubiertos por cartografía multihaz (*multibeam mapping*) en la zona de Kostarrenkala. Mediante una draga *box corer* y un trineo se han muestreado por primera vez las comunidades bentónicas y suprabentónicas de tres de estos *pockmarks*. Excepto en un único ejemplar de bivalvo thyasírido, en ninguna de las restantes especies recolectadas se conoce que hospeden bacterias simbióticas, ni que habite en ambientes con emanaciones frías (*seeping environments*). La aparente ausencia de emisiones fluidas en la columna de agua, la falta de concreciones carbonatadas en el fondo de estas depresiones, y la similitud de su composición faunística con la de otras comunidades bentónicas del talud de áreas adyacentes llevan a pensar que los tres *pockmarks* estudiados deberían ser considerados como depresiones fósiles inactivas. Sin embargo, tal conclusión no puede hacerse extensiva a los otros *pockmarks* más profundos situados en el área, donde en imágenes de vídeo se han detectado aguas turbias cercanas al fondo. Por consiguiente, si se quiere lograr una mejor comprensión de su actual actividad de emisión, sería necesario llevar a cabo más investigaciones en estas depresiones profundas.

• PALABRAS CLAVE: *Pockmark*, comunidades bentónicas, Océano Atlantico NE, Golfo de Vizcaya, caladero de Kostarrenkala.

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INTRODUCTION

Pockmarks were first described by Canadian marine geologists (King and MacLean, 1970) in muddy bottoms of the Scotian Shelf and subsequently found world-wide in many marine environments at depths of between 6 and 4800 m (Fader, 1991). Pockmarks are depressions in the seabed, generally circular or ellipsoidal at the top (from 1 m to 1 km long) and more or less regularly cone-shaped in cross–section, with a maximum central bottom depth ranging between 0.5 and 58 m. It is generally believed that they are formed by rapid expulsion of liquid (groundwater in coastal areas) or gas (methane seeping) through seafloor sediments (Dando, 2001; Gillet *et al*., 2008). The escaping gas may originate either from the microbial decomposition of organic matter within the near-seabed sediments (microbial methane) or from the thermocatalytic destruction of kerogens deep within the sediments (thermogenic gases: methane as well as higher hydrocarbon gases). Aside from the consequences of its expulsion (greenhouse effect, slope instability), this methane-rich fluid may be the principal source of energy for highly productive benthic communities. Active pockmarks are known to shelter chemosynthetic animals (some thyasirid and lucinid bivalves as well as mouthless and gutless nematodes, all containing endosymbiotic bacteria). However, stable isotopic analyses of pockmark benthic animals have indicated that methane-derived carbon contributes little to their nutrition (Dando *et al*., 1991). Furthermore, in active pockmarks, rock–like concretions (crusts, slabs, etc.) are known to occur sometimes on the seabed, due to the cementation of sediment particles by methane-derived carbonates. These new hard substrates allow the settlement of allochthonous epifaunal species (mainly anthozoans, but also hermit crabs, echinoderms, etc.) and the subsequent attraction of their predators, thus contributing to the enhancement of pockmark benthic biodiversity and biomass with respect to surrounding areas (Judd, 2001).

So far, few studies have focused on pockmark benthic communities in relation to methane seeping activity. The pioneer study of Dando *et al.* (1991) was focused on the macro-infaunal community of the Scanner pockmark, an active depression 18.5 m deep, which lies at a depth of 150 m in the northern North Sea. The seeping activity of this pockmark was demonstrated by the presence of a plume of gas 60 m high in the water column above the depression (echo-sounding recording) and by the bottom sampling of a piece of carbonate cemented sediment containing a dead shell of the lucinid *Lucinoma borealis* (symbiotic bacteria-containing bivalve). In all, 67 taxa with combined densities ranging from 708 to 1550 ind. m^{-2} were found.

Gomes Sumida *et al.* (2004) listed the benthic fauna of 3 inactive pockmarks located on the slope off SE Brazil (ca. 700 m water depth). Two dredge transects were carried out throughout these depressions (mix of benthic taxa from inside and outside the pockmarks). The benthic assemblage was numerically dominated by Ophiuroidea (73%), followed by Cirripedia (9%) and Polychaeta (6%). From the total of 94 species identified, only one of them (an ampharetid polychaete) was considered truly endemic to reducing environments.

More recently, Wildish *et al.* (2008) intensively investigated the benthic macroinfauna of 17 pockmarks located at depths of between 35 and 81 m in Passamaquoddy Bay on Canada's Atlantic coast. These shelf depressions were elliptical and cone-shaped, with a depth range between 5.1 and 50.8 m, most of them with a central flat bottom. Gas bubbling was rarely observed, and authigenic carbonate-cement bioherms were not detected on the bottom of these structures. Nevertheless, the presence of sulphide in the sediment cores down to 1 m depth below bottom surface, the occasional presence of white patches of the filamentous bacteria *Beggiatoa* sp. at the sediment-water interface, and the sampling of a few individuals of *Thyasira flexuosa* and *Solemya* sp. (bivalves reported to carry chemosynthetic bacteria in their gill tissues; see Southward, 1986) suggest at least episodic seeping activities for these pockmarks. The pockmark benthic communities showed major or minor structural differences from reference communities located outside the pockmarks, depending on their equilibrium level with respect to seeping activity. Two groups of pockmarks were identified: some at various stages in a pre-equilibrium succession (low values of species richness and macro-infaunal density), others in an equilibrium stage comparable to reference communities (significantly higher species richness and density values).

A recent multibeam mapping of the Capbreton canyon (Bourillet *et al*., 2007; Gillet *et al*., 2008) revealed the presence of many slope pockmarks (> 45 units) on its southern margin (Kostarrenkala fishing grounds). As shown in Fig.1, these pockmarks are located on the middle part of the upper slope at depths of between 400 and 800 m, and most of them are cone-shaped in cross-section. According to Gillet *et al.* (2008), the small pockmarks (diameter < 20 m) are randomly distributed whe-

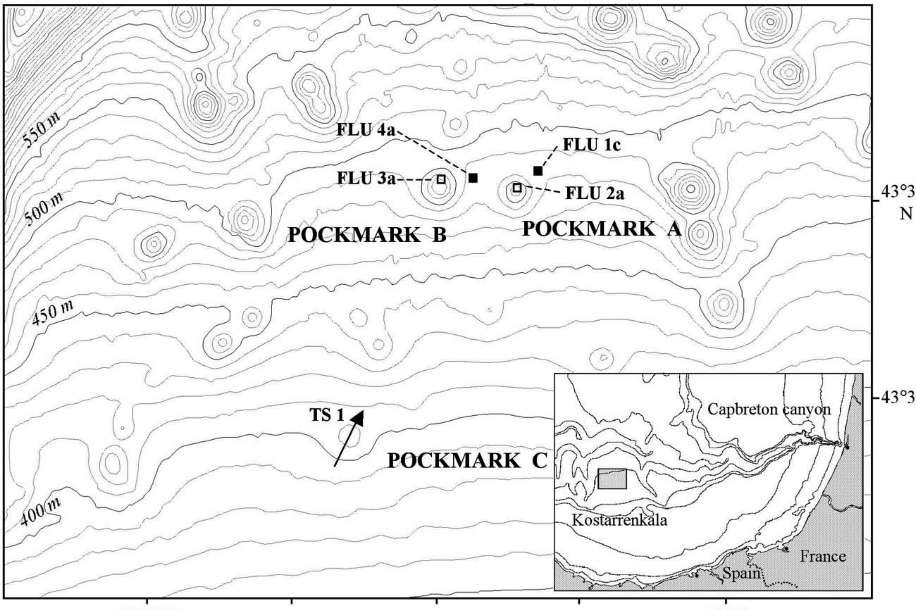

Figure 1.- Pockmark sampling sites A, B and C on the southern margin of the Capbreton canyon (Kostarrenkala fishing ground), SE Bay of Biscay. Square: box corer samples (FLU code); closed symbol: outside pockmark; open symbol: inside pockmark. Arrow: sledge sample (TS code)

reas the larger ones (ranging from 200 to 600 m in diameter) are distributed along NS alignments (faults) that extend down to the Capbreton thalweg. Some of these pockmarks trains are connected to hemi-circular scarps located at the edge of the canyon, suggesting a relation between pockmarks and slope instabilities. The main objective of the PROSECAN IV cruise (May 2007) was to investigate the geochemistry and biology of some of these pockmarks in order to distinguish between active and inactive structures. Geochemical analyses carried out on sediment cores will be published elsewhere. The present paper only focuses on the structure of their benthic communities, as related to possible seeping activity, and on their faunal peculiarities in comparison to adjacent slope communities previously studied in the same area (Marquiegui & Sorbe, 1999; Corbari & Sorbe, 2001; Frutos & Sorbe, unpublished data).

MATERIAL AND METHODS

Only 3 slope pockmarks of the Kostarrenkala area were investigated during the PROSECAN IV cruise (Fig. 1 and Table I). The choice of these structures was dictated by logistic constraint (wire length available on the boat). Their position and maximum depth was inferred from the new multibeam map of the Capbreton canyon published by Bourillet *et al.* (2007).

- Pockmark A; maximum depth: ca. 512 m (map estimate); central position: 43°35.056’N-2°16.408’W; depression depth: ca. 28 m; box corer sampling on its flank at ca. 15 m above the maximum recorded depth (inner station) and on its outer margin (outer station).
- Pockmark B; maximum depth: ca. 525 m (map estimate); central position: 43°35.070’N-2°14.932’W; depression depth: ca. 35 m; box corer sampling on its

Pockmark	Station Code	Date d/m/y	Hour h:m	Position N	Position W	Depth m
A	FLU 1c	18/5/07	14:27	43°35.149'	- 2°16.244'	483
	FLU 2a	18/5/07	14:50	43°35.139'	- 2°16.358'	497
B	FLU 3a	18/5/07	15:43	43°35.154'	- 2°16.919'	516
	FLU 4a	19/5/07	08:13	43°35.153'	- 2°16.682'	486
C	TS 1	19/5/07	11:15 [a]	43°33.705'	- 2°17.651'	391
			11.20 [b]	43°33.824'	- 2°17.594'	405

Table I - Main characteristics of the pockmark sampling stations on the southern margin of the Capbreton canyon during the PROSECAN IV cruise.
FLU: Flusha box corer; TS: suprabenthic sledge; a, b: hour, coordinates, depth at the beginning and at the end of the sledge haul on the bottom

flank at ca. 9 m above the maximum recorded depth (inner station) and on its outer margin (outer station).

- Pockmark C; maximum depth: >410 m (map estimate); central position: 43°33.831'N-2°17.534'W; depression depth: ca. 14 m; sledge sampling throughout the depression.

The pockmark benthic communities were sampled during daytime by means of two devices, using a differential GPS for the positioning of each sampling station. The macro-infauna of pockmark A and B was sampled with a Flusha box-corer (box dimensions: 31 x 29 cm; bottom area sampled: 0.0899 m^2). The top sediment layer (ca. upper 10 cm) of each core was carefully cut off and the macro-infauna was sorted on board by washing the sediment with running seawater through a 0.5 mm mesh sieve. Additional box corer samplings were carried out at the same sites (pockmarks A and B, inner and outer sites) for biochemical as well as sediment studies, allowing further visual observations on filamentous bacteria, epibenthic macrofauna and rock-like concretions, if eventually present at the sediment-water interface. Particle size analyses on sediment subcores were subsequently conducted with Malvern equipment at the Department of Geology and Oceanography, Talence (Cremer´s data, personal communication).

The suprabenthic fauna of pockmark C was sampled with a small sledge equipped with one net (mesh-size: 440 µm; rectangular opening area, height: 34 cm, width: 50.5 cm), but not provided with an opening/closing system (non-quantitative sampling). This sledge mainly sampled the motile fauna in the 17-51 cm water layer above the seafloor. However, due to the absence of a closing system, the suprabenthic sample was probably contaminated by pelagic organisms from the water column during sledge deployment and recovery. Therefore, no attempt was made to estimate the density of the organisms collected by the sledge. Furthermore, this GPS-controlled haul was carried out throughout the whole pockmark, therefore including its outer margins, flanks and base. The full contact of the sledge with the sea floor was attested by the presence of some amount of sediment in the resulting sample. The suprabenthic macrofauna collected by the net was sieved on board through 0.5 mm mesh with running sea water.

Both suprabenthic and macro-infaunal samples were preserved in a solution of formaldehyde in sea water (5%) before sorting and analysis at the laboratory.

The single suprabenthic sample carried out at pockmark C was compared with a reference sample previously taken at similar depth (397-396 m), in the same slope area (Kostarrenkala fishing ground) but at a site without pockmarks (CAPBRETON 90 cruise, Arcachon sledge, July 1990, 0-100 cm near-bottom water layer, ca. 2.8 nautical miles east of pockmark C). The Arcachon sledge model (see full description of this sampler in Sorbe, 1983) allows simultaneous quantitative sampling of the 0-50 and 50-100 cm near-bottom water layers above the sea floor. The faunal similarity between the two suprabenthic samples was estimated with the Schoener index (Schoener, 1974).

RESULTS

The three slope pockmarks investigated in the Kostarrenkala area were apparently not bubbling during our survey (no bubble detection on echo-sounding transects, at frequencies of 50 and 200 kHz) and were free of sulphide or brine in the near-bottom seawater and in the surficial sediments collected by the box corer (pockmarks A and B). Furthermore, carbonate concretions or traces of filamentous bottom bacteria were not seen at the sediment-water interface of the whole box cores examined. According to Table II, the subcore sediment analyses reveal that the 10 cm top layer of all investigated pockmark sites is silty mud (lutite contribution ranges between 54.6% and 85.8%, with a preponderance of the coarser silt fraction in most subsamples). There are, however, two notable exceptions exemplified by the interface subsamples from the outer margin of both pockmarks: higher mean and median grain size values and a lower non-dominant lutite contribution with values of 38.4% and 47.2% at pockmarks A and B, respectively. Such distinctive features suggest hydrodynamical processes more intense at the edges of these pockmarks than toward their bases.

Pockmark	Station	Depth cm	Mz µm	Md µm	Granulometric classes (%) <7 µm	7-63 µm	>63 µm
A	FLU 01b	0	67.1	85.7	9.2	29.2	61.6
		1-10	31.3	41	20.5	42.9	36.5
	FLU 02b	0	19.5	24.9	21.6	61.4	17.0
		1-10	20	26.3	21.2	60.9	17.9
B	FLU 03b	0	19.5	25.1	21.0	62.9	16.1
		1-10	20.5	27.1	20.7	61.0	18.3
	FLU 04b	0	49.2	67.4	11.6	35.6	52.7
		1-10	30.2	41.9	20.2	42.9	36.9

Table II.- Granulometric characteristics of surficial sediments taken with a Flusha box corer at pockmarks A and B from the southern margin of the Capbreton canyon during the PROSECAN IV cruise. Interface values (0 cm) and mean values for the 1-10 cm sediment layer (7 subsamples).

Mz: mean grain size; Md: median grain size

The species and densities for the macro-infauna sampled with the Flusha box corer at pockmark A and B are listed in Table III. Although without statistical significance, species richness and density values recorded at the inner and outer stations of each pockmark are on the same order of magnitude, with a similar pattern of higher values at the inner station of both depressions. In total, 35 species were

	Pockmark A				Pockmark B			
	FLU 1c		FLU 2a		FLU 3a		FLU 4a	
	N	D	N	D	N	D	N	D
TAXA								
SIPUNCULA								
Golfingia sp.	-	-	-	-	-	-	-1	11.1
Onchnesoma steenstrupi	-	-	2	22.2	2	22.2	1	11.1
ANNELIDA POLYCHAETA								
Polynoidae unid.	-	-	-	-	1	11.1	-	-
Ancistrosyllis groenlandica	-	-	2	22.2	1	11.1	-	-
Nephtys incisa	1	11.1	-	-	-	-	-	-
Nephtys sp.	3	33.4	7	77.9	4	44.5	1	11.1
Glycera mimica	1	11.1	-	-	2	22.2	1	11.1
Paradiopatra hispanica	1	11.1	-	-	-	-	-	-
Augeneria algida	-	-	5	55.6	1	11.1	-	-
Dorvilleidae unid.	-	-	-	-	1	11.1	-	-
Prionospio steenstrupi	2	22.2	-	-	-	-	1	11.1
Prionospio sp.	1	11.1	-	-	-	-	-	-
Aricidea mirunekoa	2	22.2	4	44.5	4	44.5	-	-
Paradoneis bathyilvana	-	-	1	11.1	-	-	-	-
Paradoneis mikeli	-	-	-	-	1	11.1	-	-
Levinsenia flava	2	22.2	-	-	1	11.1	1	11.1
Levinsenia gracilis	-	-	-	-	1	11.1	-	-
Levinsenia kantauriensis	-	-	-	-	1	11.1	-	-
Ophelina sp.	-	-	-	-	1	11.1	-	-
Scalibregma inflatum	-	-	1	11.1	-	-	-	-
Notomastus sp.	-	-	-	-	1	11.1	3	33.4
Flabelligena gascognensis	1	11.1	2	22.2	-	-	-	-
Eclysippe vanelli	2	22.2	-	-	1	11.1	4	44.5
Lysilla sp.	-	-	-	-	1	11.1	-	-
MOLLUSCA BIVALVIA								
Nuculoma tenuis	1	11.1	1	11.1	1	11.1	-	-
Axinulus croulinensis	1	11.1	-	-	-	-	-	-
CRUSTACEA								
Amphipoda								
Tryphosella caecula	-	-	1	11.1	-	-	-	-
Metaphoxus simplex	-	-	1	11.1	-	-	-	-
Cumacea								
Eudorella truncatula	-	-	-	-	1	11.1	-	-
Campylaspis verrucosa	1	11.1	-	-	-	-	-	-
Isopoda								
Ilyarachna longicornis	1	11.1	-	-	-	-	-	-
Tanaidacea								
Tanais cf. *dulongii*	-	-	-	-	-	-	1	11.1
Decapoda								
Calocaris macandreae	-	-	-	-	-	-	1	11.1
ECHINODERMATA								
Spatangoida	-	-	-	-	-	-	1	11.1
Leptosynapta sp.	-	-	-	-	1	11.1	-	-
Σ	20	222.1	27	300.1	27	299.9	16	177.8

Table III.- Abundance (N: number of individuals; D: density in ind. m^{-2}) of the macro-infauna sampled with a Flusha box corer inside and outside the pockmarks A and B from the southern margin of the Capbreton canyon during the PROSECAN IV cruise recorded in the 4 samples examined, belonging to Polychaeta (22 sp.), Sipunculida (2 sp.), Bivalvia (2 sp.), Amphipoda (2 sp.), Cumacea (2 sp.), Echinodermata (2 sp.), Isopoda (1 sp.), Tanaidacea (1 sp.) and Decapoda (1 sp.). Species richness ranged between 11 (base of pockmark A) and 19 species (base of pockmark B). Densities ranged between 177.8 ind. m^{-2} (flank of pockmark B) and 300.1 ind. m^{-2} (flank of pockmark A). At both the inner and outer stations of the 2 pockmarks, the infaunal community was dominated by Polychaeta (species richness: 6-15 species; percentage contribution to total density: 68.8%-81.5%). Four of these polychaetes (the paraonids *Aricidea mirunekoa*, *Paradoneis bathyilvana*, *P. mikeli*, *Levinsenia kantauriensis*) are new species recently described by Aguirrezabalaga & Gil (2009), from benthic material sampled in the Capbreton canyon, outside pockmarks. Their presence both within and outside pockmarks (see Table III) suggests that they belong to the background benthic community of this canyon and are not indicative of methane seeping activity. In addition to alive benthic species, samples also contained fish otoliths (density range: from 0 to 77.9 otoliths m^{-2} at the inner and outer stations of pockmark A, respectively).

The suprabenthic species sampled with the sledge throughout pockmark C are listed in Table IV. In this sample alone, 1352 individuals were recorded, distributed among 56 species belonging to Amphipoda (26 sp.), Mysidacea (11 sp.), Decapoda (6 sp.), Isopoda (5 sp.), Euphausiacea (4 sp.), Cumacea (3 sp.) and Pisces (1 sp.). According to their relative contribution to total abundance, these major groups were ranked as follows: Euphausiacea (37.5%), Amphipoda (36.0%), Isopoda (14.4%), Decapoda (6.1%), Mysidacea (5.1%), Pisces (0.5%) and Cumacea (0.4%). The five numerically dominant species represented 70.7% of total abundance: unidentified furcilia larvae of euphausiids (34.1%), *Orchomenella nana* (14.5% - amphipod), *Munnopsurus atlanticus* (11.6% - isopod), *Rhachotropis caeca* (7.0% - amphipod) and *Halice abyssi* (3.5% - amphipod). Not identified at species level, the furcilia larvae (mix of different species) were probably sampled not only in the near-bottom environment but also in the water column during sledge deployment and recovery (sledge without net closing system); this would explain their dominance in the sample. This taxon was therefore discarded in subsequent comparisons between suprabenthic communities from pockmark C and those from adjacent slope areas.

DISCUSSION

First of all, it must be emphasized that the two sampling procedures (box corer, sledge) carried out during this study were complementary, each giving a peculiar insight into benthic macrofaunal assemblages. As usually observed elsewhere, polychaetes were numerically dominant in the macro-infaunal community (some of them recently described as new to science) whereas amphipods ranked first in the

TAXA	N	%
CRUSTACEA		
Mysida		
Boreomysis arctica	2	0.15
Boreomysis megalops	1	0.07
Anchialina agilis	2	0.15
Atlanterythrops crassipes	9	0.67
Erythrops neapolitana	8	0.59
Paramblyops rostrata	10	0.74
Parapseudomma calloplura	11	0.81
Leptomysis gracilis	1	0.07
Mysideis parva	6	0.44
Mysidetes farrani	11	0.81
Mysidella biscayensis	3	0.22
unid.*	5	0.37
Amphipoda		
Amphilochoides boecki	3	0.22
Eusirus leptocarpus	2	0.15
Rhachotropis caeca	94	6.95
Rhachotropis integricauda	11	0.81
Rhachotropis glabra	5	0.37
Rhachotropis grimaldii	3	0.22
Rhachotropis spp.*	2	0.15
Hippomedon denticulatus	9	0.67
Orchomenella nana	196	14.5
Podoprion bolivari	1	0.07
Scopelocheirus hopei	12	0.89
Sophrosyne hispana	1	0.07
Trischizostoma nicaeense	1	0.07
Tryphosella cf. *longidactyla*	10	0.74
Cheirocratus intermedius	11	0.81
Bathymedon monoculodiformis	2	0.15
Bathymedon sp.*	1	0.07
Halicreion aequicornis	7	0.52
Monoculodes acutipes	1	0.07
Synchelidium maculatum	3	0.22
Amphipoda (continued)		
Halice abyssi	47	3.48
Nicippe tumida	2	0.15
Harpinia laevis	1	0.07
Andaniopsis nordlandica	36	2.66
Stegocephaloides auratus	13	0.96
Syrrhoe affinis	10	0.74
Themisto compressa	1	0.07
Primno brevidens	1	0.07
Cumacea		
Diastyloides biplicata	2	0.15
Mesolamprops denticulatus	2	0.15
Campylaspis glabra	2	0.15
Isopoda		
Disconectes phalangium	1	0.07
Ilyarachna longicornis	7	0.52
Munnopsurus atlanticus	157	11.61
Natatolana borealis	29	2.14
Gnathia sp. (praniza)	1	0.07
Euphausiacea		
Euphausia krohni	10	0.74
Meganyctiphanes norvegica	13	0.96
Nematoscelis megalops	15	1.11
Stylocheiron longicorne	8	0.59
Furcilia unid.	461	34.1
Decapoda		
Philocheras echinulatus	3	0.22
Dichelopandalus bonnieri	1	0.07
Pandalina profunda	3	0.22
Pasiphaea sivado	35	2.59
Processa nouveli holthuisi	38	2.81
Solenocera membranacea	2	0.15
PISCES		
Juvenile unid.	7	0.52
Σ	1352	100

Table IV.- Abundance (N: number of individuals) and dominance (%) of the suprabenthic species sampled with a sledge (net mesh size: 440 µm) towed throughout pockmark C (sample TS1; 391-405 m depth) from the southern margin of the Capbreton canyon during the PROSECAN IV cruise.

*: damaged specimens

near-bottom water community (no species new to science in the suprabenthic compartment of the pockmark benthic ecosystem). None of these macro-infaunal or suprabenthic species were previously mentioned as known components of deep cold-seep communities (see species list in Sibuet and Olu, 1998). Furthermore, none of them were considered symbiont-containing taxa, with the exception of the small thyasirid bivalve *Axinulus croulinensis*, known to host a few symbiotic bacteria on their gills (Dufour, 2005) but never associated with any specific reducing environment (Payne and Allen, 1991). The low abundance of this bivalve (only 1 specimen caught during the present survey) demonstrates the negligible functional role of these symbiotic taxa within the benthic ecosystem of the pockmarks here studied. Surprisingly, the only tanaid specimen collected by the box corer on the outer margin of pockmark B (486 m water depth) was morphologically indistinguishable from the cosmopolitan species *Tanais dulongii* (G. Bird, personal communication). This common species is known to live in exposed tidal hard-bottom habitats where it inhabits self-constructed tubes of sand grains and detritus fragments (Holdich and Jones, 1983; Hamers and Franke, 2000). The present finding of this tanaid in bathyal muddy bottoms is quite unusual (new sibling species or drifting specimen?).

No bioherm fragments (carbonate consolidated sediments) were observed in the Flusha cores from the inner and outer stations of pockmarks A and B and, consequently, no associated epifaunal organisms were detected in these samples. Fish otoliths were present in some cores, but only in low densities, not comparable to the high values mentioned by Dando *et al.* (1991) on the bottom of the Scanner pockmark (range: 540-3690 otoliths m^{-2}). Such high otolith abundances were thought to result from sediment displacement and winnowing of the lighter fractions after catastrophic gas or liquid expulsions. Observed values of species richness for macro-infauna are comparable to values given by Dando *et al.* (1991) for the Scanner pockmark (range: 15-24 species core^{-1}), with a dominance of polychaete species in both cases. However, they are lower than values given by Wildish *et al.* (2008) for the Passamaquoddy Bay pockmarks (range: 22-44 species core^{-1}). Observed total densities for macro-infauna are significantly lower than values recorded by Dando *et al.* (1991) for the Scanner pockmark (range: 708-1550 ind.m^{-2}) and especially by Wildish *et al.* (2008) for the Passamaquoddy Bay pockmarks (range: 1361-1494 ind.m^{-2} for communities in a pre-equilibrium stage; 2639-5230 ind.m^{-2} for communities considered to have reached an equilibrium stage). These higher diversity and abundance values are probably related to the distinct local oceanographic conditions within these shelf pockmarks in comparison to the Capbreton slope pockmarks, which are located in a less productive area. All the benthic species sampled by the box corer have been recorded elsewhere in the Capbreton canyon, including non-pockmark areas. Furthermore, no symbiont-containing species such as the highly specialized bivalves *Thyasira sarsi* (Thyasiridae) and *Lucinoma borealis* (Lucinidae) mentioned by Dando *et al.* (1991) and Dando

(2001) for the Scanner pockmark [see also Sibuet and Olu (1998) for deep cold-seep communities] were detected in the core samples herein examined. Similarly, the deep bivalve *Modiolaria fisheri* (Mytilidae) was not recorded in the core samples examined, although it was recently re-discovered at ca. 860 m water depth on muddy sediments of the Capbreton thalweg (Sorbe *et al*., 2001; Le Pennec *et al*., 2005). Such mytilid bivalves are known to occur as ring belts at the top of some active pockmarks. Histological investigations carried out on different organs of *M. fisheri* (gills, digestive tract, etc.) demonstrated that this deep mytilid is not a symbiont-containing species, consuming organic particles issued from the photic area (pelagic diatoms, cocolithophorids, etc.) on a heterotrophic pathway (Le Pennec *et al*., 2005).

The single suprabenthic sample from pockmark C was compared with another carried out at similar depth (397 m), in the same area but in a site without pockmarks (CAPBRETON 90 cruise, sample TS8, Arcachon sledge, July 1990, 0-100 cm near-bottom water layer). Excluding the furcilia larvae (see above), the Schoener index of similarity between the two suprabenthic samples was 46.6%, thus demonstrating that pockmark and surrounding bathyal assemblages are not markedly different in their structural composition. Furthermore, as in the case of the macro-infaunal components, all the suprabenthic species sampled by the sledge have been recorded elsewhere in the Capbreton canyon. Surprisingly, a few species registered in this sample (the shelf mysids *Anchialina agilis* and *Leptomysis gracilis*; the shelf break amphipod *Rhachotropis integricauda*) are known to live normally in shallower habitats. They are probably isolated specimens swept away from the shelf and collected in surficial water layers by the non-closing net of the sledge.

CONCLUSIONS

The absence of rock-like carbonate concretions and associated patches of filamentous bacteria at the seabed, the absence of specialized symbiont-containing species in benthic communities (except for 1 specimen of the bivalve *Axinulus croulinensis*) and the similarity of community structure with surrounding slope areas combine to suggest that the 3 pockmarks A, B and C investigated in the Kostarrenkala area should be considered inactive fossil depressions. However, we do not know if they are representative of the other pockmarks identified in the same area. Near-bottom turbid waters detected by video recordings around deeper structures during the PROSECAN IV cruise (H. Gillet, personal communication) suggest that further investigations need to be carried out on these deep depressions for a better understanding of their actual seeping activity.

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