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SPECIAL TOPIC

Megabenthic diversity patterns and community structure of the Blanes submarine canyon and adjacent slope in the Northwestern Mediterranean: a human overprint?

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Abstract

The composition and structure of megabenthic communities in the Blanes canyon and adjacent open margin (Northwestern Mediterranean) were studied. The aim was to assess the effect of the canyon and commercial fishing intensity on the community composition and structure of benthic megafauna by (i) describing the megabenthic community composition, (ii) quantifying faunal abundance and biomass and (iii) describing community structure with MDS analyses and biodiversity indices. The results are compared between three sites (canyon head, canyon wall and open margin) located between 435 m and 700 m. Samples were collected using a commercial bottom trawl between April 2003 and March 2004. These sites are exploited by the local fishing fleet that targets the rose shrimp *Aristeus antennatus*. A total of 131 megabenthic species were identified from the three sites, with fishes and decapod crustaceans being the most speciose, most abundant and of higher biomass. The species richness, abundance and biomass of non-crustacean invertebrates were low. There were no significant differences in total abundance and biomass between the three sites. However, community structure analysis suggests that the open margin community is significantly different from the canyon head and canyon wall, with a lower species richness, lower diversity and lower evenness. The open margin community also reflects a higher degree of disturbance compared to the two canyon habitats. The results indicate that there is a canyon effect on the community structure of benthic megafauna, but this may be modulated by differing fishing pressure, which adds an additional factor to margin heterogeneity.

Problem

Local and regional-scale sampling have provided most of the present information available on benthic deep-sea biodiversity patterns. In the late 1960s, the first evidence of high biodiversity in the deep sea was provided (Hessler & Sanders 1967; Sanders 1968) and although sampling is still limited at bathyal and abyssal depths, many studies have followed to investigate local and regional diversity patterns. Our present knowledge of regional patterns of deep-sea biodiversity has been reviewed by Rex (1981) and Levin *et al.* (2001) and the effect of the habitat's spatio-temporal variations in large-scale diversity by Stuart *et al.* (2003). Regional deep-sea diversity patterns show clear geographic variations on spatial scales between 100 and 1000 km, with unexpected complexity of community structure. These patterns of biodiversity are shaped by environmental factors where food availability, substrate and sediment type, hydrologic conditions and catastrophic events play a central role (Levin *et al.* 2001; Gage 2003; Smith *et al.* 2008). However, most deep-sea diversity studies have been conducted on macrofauna, focusing on a few taxa and a limited number of geographic areas. Very little is known about meiofauna and megafauna diversity patterns, as well as community structure in deep-sea habitats (Levin *et al.* 2001) and the factors that sustain very high levels of local diversity (Etter & Mullineaux 2001; Snelgrove & Smith 2002).

In the deep Mediterranean Sea, little information is available on diversity patterns and community structure of benthic macro- and megafauna. Studies on the macrofauna of the Levantine basin (Eastern Mediterranean) show that benthic biomass, abundance and diversity decrease significantly with depth, with major transitions at 200, 500 and 1000 m (Tselepides *et al.* 2000; Basso *et al.* 2004). In the Western Mediterranean Basin, most studies on deep-sea megafauna have described the biology and ecology of specific groups, often related to species of commercial value such as the rose shrimp *Aristeus antennatus* and ecologically associated species (Cartes & Sardà 1993; Demestre 1995; Company *et al.* 2001, 2003, 2004, 2008; Puig *et al.* 2001; D'Onghia *et al.* 2004; Sardà *et al.* 2004b; Ramirez-Llodra *et al.* 2007). Studies investigating diversity patterns, community structure and distribution of Mediterranean deep-sea fauna (Sardà *et al.* 2009) have focussed on the two most abundant groups below 600 m depth: fishes (Stefanescu *et al.* 1993; Sardà *et al.* 1994a; Moranta *et al.* 1998; D'Onghia *et al.* 2004) and decapod crustaceans (Abelló *et al.* 1988; Cartes & Sardà 1992, 1993; Cartes *et al.* 1994; Sardà *et al.* 1994a; Maynou & Cartes 2000; Company *et al.* 2004). However, the much less abundant non-crustacean benthic megafauna is virtually unstudied in terms of its diversity patterns, with the exception of a few descriptive studies (Fredj & Laubier 1985; Pérès 1985; Laubier & Emig 1993) and scarce quantitative data (Ramirez-Llodra *et al.* 2008).

Continental margins around the world's oceans are often carved by submarine canyons that form major topographic features incising the shelf and margin. Canyons act as major conduits for transport and concentration of particles (Heussner *et al.* 1996; Puig *et al.* 2003) and macrophytes (Vetter & Dayton 1999) to bathyal and abyssal depths, and can enhance the intensity of catastrophic events such as deep-water cascading (Canals *et al.* 2006). Because of their rugged topography, canyons shape local current dynamics (Durrieu de Madron *et al.* 1996; Turchetto *et al.* 2007; Flexas *et al.* 2008). These modified currents can influence benthopelagic faunal distribution patterns by modulating disturbance intensity over the sea floor (Sardà *et al.* 1994a,b, 2009b) and result in increased abundance and diversity of pelagic species (Gili *et al.* 1999; Albaina & Irigoien 2007). Habitat complexity and increased organic matter in canyons may also affect species composition and increase the abundance and biomass of benthic species in canyons (Rowe *et al.* 1982; Vetter & Dayton 1999; Wei *et al.* in press). It can also provide favourable areas for recruitment and maintenance of benthic megafauna species, including those of commercial value (Sardà *et al.* 1994a,b; Stefanescu *et al.* 1994; Sardà & Cartes 1997; Tyler & Ramírez-Llodra 2002).

The Northwestern Mediterranean margin is characterised by the presence of numerous submarine canyons *e.g.* Merenguera, Foix, Palamós, Blanes and Gulf of Lions canyons (Canals *et al.* 1996; Canals 1998). Many of these canyons have been studied in terms of geomorphology and physical processes (Heussner *et al.* 1996; Puig & Palanques 1998; Puig *et al.* 2000, 2003; Bethoux *et al.* 2002; Canals *et al.* 2006; Flexas *et al.* 2008) but only a few studies have focused on biological aspects (Sardà *et al.* 1994a, 2009b; Ramirez-Llodra *et al.* 2008). In particular, the Blanes canyon (Fig. 1) has been intensively studied over an annual cycle under the *RECS II* project (Sardà *et al.* 2009b). This study focused on the investigation of flow dynamics (Flexas *et al.* 2008), particle flux dynamics (Zúñiga *et al.* in press), spatio-temporal variations in meiobenthic densities (J. Coenjaerts, unpublished data) and abundance and distribution of the commercial shrimp *A. antennatus* related to environmental variables (Sardà *et al.* in press). The Blanes canyon is the largest in the Catalan Sea, oriented in a NW–SE direction. The head of the canyon is less than 4 km offshore, cuts the continental platform at 60 m depth (Díaz & Maldonado 1990) and is linked with the Tordera River. The canyon has a V-shaped cross-section in the upper region, indicating high erosion, and a U-shape cross-section in the lower region, representative of higher sediment deposition. Flexas *et al.* (2008) and Zúñiga *et al.* (2009) have shown that the Northern Current, or incoming slope current, is the main source of variability, with deep flow intensifications inside and along the axis of the canyon caused by Northern Current offshore displacements. The topography of the canyon walls play a major role in current variability within the canyon, with a highly variable flow over the eastern smooth wall and an unidirectional offshore flow over the western wall forced by its shallower and sharper topography (Flexas *et al.* 2008). These topographic and current patterns have significant impacts on the particle flux dynamics, where the more stable conditions of the western flank result in steadier sedimentary processes, whereas the active eastern region enhances erosion (Zúñiga *et al.* 2009). The canyon head region has the highest near-bottom downwards particle flux, with a threefold higher flux than at the open margin (Zúñiga

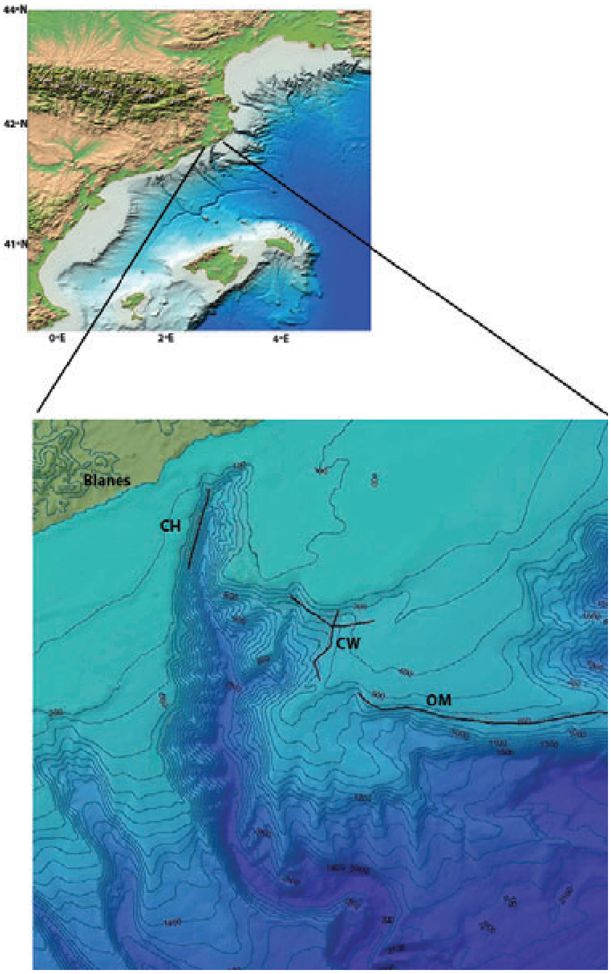

Fig. 1. Map of the Catalano-Balearic Sea and an amplification of the Blanes region, showing the bathymetry of the canyon and adjacent margin and the location of the three study sites. CH = canyon head; CW = canyon wall; OM = open margin. Dark lines show the trawled areas. Catalano-Balearic Sea map modified from: 2005, Catalano-Balearic Sea – Bathymetric Chart, http://www.icm.csic.es/geo/gma/MCB/index.htm.

et al. 2009). Effects of variations in hydrodynamics and particle flux in Blanes canyon and adjacent slope have been related to spatio-temporal variations in meiobenthos density and distribution (Coenjaerts *et al.* unpublished data) and occurrence of *A. antennatus* (Sardà *et al.* 2009).

As for many other canyons (Martín *et al.* 2008; Schlacher *et al.* 2010), the Blanes canyon and adjacent margin are important fishery areas, with bottom trawl activities often affecting faunal communities still poorly understood. In the Blanes canyon, the specialised commercial fleet targets *A. antennatus* (Sardà *et al.* 2009), one of the main marine resources in the Western Mediterranean, which has been intensively fished year-round for over 60 years in and around the Blanes canyon by a local specialised fleet between 600 and 800 m depth. The fishery is mainly centered on the open margin from late winter to early summer and also in the eastern canyon walls from late summer to mid-winter (Company *et al.* 2008; Sardà *et al.* 2009b), with recent incursions on the axis of the canyon head. The western walls of the canyon are not fished because of their steep and rough topography.

The aim of this study is to assess the effect of the Blanes canyon on the community composition and structure of benthic megafauna, to determine whether the observed diversity patterns define the canyon as a distinct system within the bathyal margin habitat. Two major scientific questions were addressed in this study: (i) Are there differences in biomass and abundance of benthic megafauna between the three habitats considered (canyon head, canyon wall and open margin)? (ii) Are community structure and diversity affected by the presence of the canyon and/or by commercial fishing? The results are discussed in relation to topographic and environmental factors of the Blanes canyon and adjacent slope and the effects of fishing pressure in the area.

Material and Methods

Sampling area and methods

This study is part of the project *RECS II*, which conducted an integrated study of the Blanes canyon (41°34′ N, 02°50′ E) and adjacent slope (41°15′ N, 02°48′ E) in relation to the exploitation of the rose shrimp *Aristeus antennatus*. The samples were collected by commercial fishing bottom trawlers in three habitats: (i) the Blanes canyon head (CH) with an average depth of 514 m; (ii) the western canyon wall (CW) with an average depth of 527 m; and (iii) the adjacent open margin (OM) with an average depth of 619 m (Fig. 1). These areas are main target sites for the *A. antennatus* fishery. Benthic megafauna (considering here benthic and epibenthic invertebrates as well benthic and benthopelagic fishes) was sampled with commercial bottom otter trawls with a mouth opening of 35 m and a 6-mm side mesh cod-end liner, trawled over the seabed at approximately 1.8–2 knots. The start and end positions of each trawl, as well as the horizontal opening of the gear, were measured with SCANMAR sensors mounted on the trawl's mouth, allowing calculation of area sampled. The sampling was conducted during seven cruises covering the four seasons of an annual cycle between April 2003 and April 2004 (Table 1). Megafauna samples were sorted to species level whenever possible, or to the smallest taxonomical level possible otherwise. The biomass (wet weight, g) and

Cruise code	Date	Sampling depth, m (area sampled, km^2) CH	CW	OM	Season
M1	14/04/03	585 (0.17)	585 (0.19)	600 (0.33)	SPR
M2	29/05/03	576 (0.16)	603 (0.24)	667 (0.53)	SPR
M4	20/08/03	364 (0.15)	520 (0.30)	700 (0.48)	SUM
M5	30/09/03	502 (0.24)	567 (0.24)	631 (0.24)	AUT
M7	17/12/03	475 (0.17)	402 (0.35)	512 (0.46)	WIN
M9	10/03/04	585 (0.25)	567 (0.35)	640 (0.36)	SPR
M11	21/04/04	*	585 (0.28)	695 (0.53)	SPR

CH, canyon head; CW, canyon wall; OM, open margin; SPR, spring; SUM, summer; AUT, autumn; WIN, winter. *No sample.

Table 1. Sampling information, including dates, trawls conducted per habitat with site depth (m) and area sampled (km^2), and related season.

abundance as number of individuals (N) were calculated and standardised per area sampled (g·km^{-2} and N·km^{-2}).

Community analyses

The species presence–absence information collected from the three habitats (CH, CW, OM) is compiled in Table 2. The abundance (N·km^{-2}) and biomass (g·km^{-2}) data are reported per phylum, with the exception of the Chordata, which was subdivided into Classes Chondrichthyes and Actinopterygii (here also referred to as teleostean fishes), as well as the less abundant Ascidiacea and Thaliacea. The abundance and biomass of each phylum (Class for the Chordata) from each sample (month/habitat) are shown in Table 3A, B. These data were then pooled per habitat and the mean and standard deviations plotted for each of the three habitats (CH, CW, OM). Ascidiaceans, thaliaceans, sipunculids and cnidarians showed very low abundance and biomass and were excluded from the graphs, with data relevant to these groups only available in Table 3A, B. The mean individual weight for each community was calculated by dividing the total weight for each species in each sample by the number of individuals in the sample and then averaging this for all species in the sample. This gives an estimation of the mean size of individuals in a community. Non-parametric analysis of variance (Kruskal–Wallis) was employed to test differences in abundance and biomass of each phylum or class (excluding sipunculids and cnidarians) between habitats and of average individual weight between habitats.

The abundance data for each species collected at the three habitats in each sampling month was used to calculate three biodiversity indices. Species Accumulation curves were plotted for each habitat (Gotelli & Colwell 2001). Shannon–Wiener diversity index (*H*') (Shannon, 1948) and Pielou's index of evenness (*J*') (Pielou 1966) were calculated for each sample (month/habitat), results were pooled per habitat and the means and standard deviations plotted. Similarity in community structure between habitats and seasons was analysed by multidimensional scaling analyses (MDS) with PRIMER-E software (Clarke & Gorley 2006), using individual trawls (month × habitat). This analysis is an iterative procedure that minimises the difference between ranked Bray–Curtis similarity values and two-dimensional distance between each pair of samples. The data matrix consisted of abundance data for all megafauna species from the three habitats (CH, CW and OM) and subject to four natural treatments (spring, summer, autumn and winter) (Table 1). The abundance data was 4th root-transformed prior analysis, to reduce dominant contribution of abundant species (Clarke & Warwick 2001). The Bray–Curtis resemblance matrix was constructed from the transformed data and CLUSTER, SIMPROF and MDS analyses applied. MDS was ran with 99 reiterations and minimum stress = 0.01. SIMPROF was run with 999 simulations and a significant level of 0.5%. ANOSIM was used to test for differences in community composition between habitats.

Ranked species abundance plots (k-dominance) were computed for abundance data pooled from all sampling months for each habitat (CH, CW and OM), where species are ranked in decreasing order and the relative abundance is plotted against rank on a log scale. ABC plots were computed, where abundance and biomass k-dominance curves are plotted on the same graph, with species ranked from most to least important in terms of abundance and biomass along the logged x-axis (Warwick & Clarke 1994; Magurran 2008). The W statistic of ABC plots, which measures the extent to which the biomass curve lies above the abundance curve, was calculated.

Results

Community composition

The benthic megafauna collected from the Blanes canyon and adjacent margin was composed of 131 species

Table 2. List of megabenthic species sampled from the Blanes canyon and adjacent margin.

PHYLUM	Class	Order	Family	SPECIES	CH	CW	OM
CNIDARIA	Scyphozoa	Semaeostomeae	Pelagiidae	*Pelegia noctiluca*	*		*
	Anthozoa	Pennatulacea	Pennatulidae	*Pennatula* sp.	*		
ANNELIDA	Polychaeta			Polychaeta ind.	*	*	
SIPUNCULA	Sipunculidea	Sipunculiforms	Sipunculidae	Sipunculid ind.		*	*
MOLLUSCA	Cephalopoda	Octopoda	Octopodidae	*Bathypolypus sponsalis*	*	*	*
				Eledone cirrhosa	*	*	*
				Eledone elongata	*		
				Pteroctopus tetracirrhus		*	
		Sepiolida	Sepiolidae	*Neorosia* sp.	*		
		Teuthida	Onychoteuthidae	*Ancistroteuthis lichtensteinii*		*	
			Chtennopterygidae	*Chenopteryx sicula*			*
			Histioteuthidae	*Histoteuthis bonnellii*		*	*
				Histoteuthis reversa	*	*	*
			Ommastrephidae	*Todarodes sagittatus*	*	*	*
		Thecosomata	Cymbuliidae	*Cymbulia peronii*	*		
ARTHROPODA	Malacostraca	Amphipoda	Phronimoidea	*Phronima sedentaria*	*	*	*
		Isopoda	Cirolanidae	*Natatolana borealis*	*	*	*
		Euphausiacea	Euphausiidae	*Meganyctiphanes norvegica*	*	*	*
		Decapoda	Alpheidae	*Alpheus glaber*	*	*	*
			Aristeidae	*Aristaeomorpha foliacea*		*	*
				Aristeus antennatus	*	*	*
			Axiidae	*Calocaris macandrae*	*	*	*
			Benthesicymidae	*Gennadas elegans*	*	*	*
			Crangonidae	*Philocheras echinulatus*	*	*	
				Polychaeles typhlops	*	*	*
				Pontocaris lacazei	*	*	*
				Pontophilus spinosus	*	*	*
			Diogenidae	*Dardanus arrosor*	*	*	*
			Dorippidae	*Medorippe lanata*		*	*
			Galatheidae	*Munida intermedia*	*	*	*
				Munida tenuimana	*	*	*
			Geryonidae	*Geryon longipes*		*	*
			Goneplacidae	*Goneplax rhomboides*	*	*	*
			Hippolytidae	*Ligur ensiferus*	*		
			Homolidae	*Paromola cuvieri*	*	*	*
			Nephropidae	*Nephrops norvegicus*	*	*	*
			Oplophoridae	*Acantephyra eximia*	*	*	*
				Acantephyra pelagica	*	*	*
			Paguridae	*Pagurus alatus*	*	*	*
				Pagurus excavatus	*	*	
				Pagurus prideauxi	*	*	
			Pandalidae	*Chlorotocus crassicornis*	*	*	
				Pandalina profunda	*	*	*
				Plesionika acanthonotus		*	*
				Plesionika edwardsii	*	*	
				Plesionika gigliolii	*	*	
				Plesionika heterocarpus	*	*	
				Plesionika martia	*	*	*
			Pasiphaeidae	*Pasiphaea multidentata*	*	*	*
				Pasiphaea sivado	*	*	*
			Penaeidae	*Parapenaeus longirostris*		*	
			Portunidae	*Liocarcinus depurator*	*	*	
				Macropipus tuberculatus	*	*	*
			Processidae	*Processa canaliculata*	*	*	*
				Processa nouvelli	*	*	*
			Sergestidae	*Sergestes arcticus*	*	*	*

Table 2. Continued.

PHYLUM	Class	Order	Family	SPECIES	CH	CW	OM
				Sergestes henseni	*	*	*
				Sergia robusta	*	*	*
			Solenoceridae	*Solenocera membranacea*	*	*	*
			Xanthidae	*Monodaeus couchi*	*	*	*
ECHINODERMATA	Echinoidea	Spatangoidea	Spatangidae	*Brissopsis lyrifera*	*		
	Asteroidea	Spinulosida	Echinasteridae	*Echinaster sepositus*	*		
	Holothuroidea	Molpadiida	Molpadiidae	*Molpadia musculus*		*	*
CHORDATA	Ascidiacea	Enterogona	Ascidiidae	*Ascidia conchilega*	*		
	Thaliacea	Pyrosomida	Pyrosomatidae	*Pyrosoma atlanticum*	*	*	*
		Salpida	Salpidae	*Salpa* sp.			*
	Chondrichthyes	Carcharhiniformes	Scyliorhinidae	*Galeus melastomus*	*	*	*
				Scyliorhinus canicula	*	*	*
		Squaliformes	Somnosidae	*Centroscymnus coelolepis*	*		
			Etmopteridae	*Etmopterus spinax*	*	*	*
	Actinopterygii	Notacanthiforme	Notacanthidae	*Notacanthus bonapartei*	*	*	*
				Polyacanthontus rissoanus	*	*	*
		Anguiliformes	Congridae	*Conger conger*	*	*	*
			Nemichthyidae	*Nemichthys scolopaceus*	*	*	*
				Nettastoma melanurum	*	*	*
			Ophichthidae	*Ophichthus rufus*	*	*	*
		Clupeiformes	Clupeidae	*Sardinapilchardus*	*		
		Osmeriformes	Alepocephalidae	*Alepocephalus rostratus*	*	*	*
			Argentinidae	*Glossanodon leioglossus*		*	
		Stomiiformes	Sternoptychidae	*Argyropelecus haemigymnus*	*	*	*
				Maurolicus muelleri	*	*	
			Stomiidae	*Chauliodus sloani*	*	*	*
				Stomias boa	*	*	*
		Aulopiformes	Paralepididae	*Arctozenus risso*	*	*	*
			Chlorophthalmidae	*Chlorophthalmus agassizi*		*	*
			Evermannellidae	*Evermannella balbo*		*	
		Myctophiformes	Myctophidae	*Lampanyctus crocodilus*	*	*	*
				Mictophidae ind.	*	*	*
				Notoscopelus elongatus		*	
				Symbolophorus veranyi	*	*	*
		Gadiformes	Gadidae	*Antonogadus megalokynodon*	*	*	*
				Gadiculus argenteus	*	*	*
				Micromesistius poutassou	*	*	*
				Molva dypterygia	*	*	*
			Macrouridae	*Caelorinchus caelorhincus*	*	*	*
				Coryphaenoides mediterraneus	*		
				Hymenocephalus italicus	*	*	*
				Nezumia aequalis	*	*	*
				Trachyrhynchus scabrus	*	*	*
			Merlucidae	*Merluccius merluccius*	*	*	*
			Moridae	*Gadella maraldi*	*		
				Lepidion lepidion	*	*	*
				Mora moro	*	*	*
			Phycidae	*Phycis blennoides*	*	*	*
		Ophidiiformes	Bythitidae	*Cataetyx alleni*	*	*	
				Cataetyx laticeps	*		
			Carapidae	*Carapus acus*	*		*
				Echiodon dentatus	*		
			Ophidiidae	*Ophidion barbatum*		*	
		Lophiiformes	Lophiidae	*Lophius budegassa*	*	*	*
				Lophius piscatorius	*	*	*
		Beryciformes	Trachichthyidae	*Hoplostethus mediterraneus*	*	*	*

Table 2. Continued.

PHYLUM	Class	Order	Family	SPECIES	CH	CW	OM
		Zeiformes	Caproidae	*Capros aper*	*	*	
		Scorpaeniformes	Liparididae	*Paraliparis leptochirus*	*	*	*
			Scorpaenidae	*Helicolenus dactylopterus*	*	*	*
			Triglidae	*Lepidotrigla cavillone*	*	*	
				Trigla lyra	*	*	
		Perciformes	Callionymidae	*Callionymus maculatus*	*	*	
			Epigonidae	*Epigonus constanciae*		*	*
				Epigonus denticulatus	*	*	*
				Epigonus telescopus	*	*	*
			Gobiidae	*Lesueurigobius friesii*	*		
			Sparidae	*Pagellus bogaraveo*		*	*
			Serranidae	*Serranus hepatus*			*
			Carangidae	*Trachurus trachurus*	*	*	
		Pleuronectiformes	Scophthalmidae	*Lepidorhombus boscii*	*	*	*
			Soleidae	*Monochirus hispidus*			*
			Cynoglossidae	*Symphurus ligulatus*	*	*	*

CH = canyon head; CW = canyon wall; OM = open margin. *Indicates occurrence of species in each habitat.

belonging to seven phyla, with 110 species sampled on the canyon head, 109 species from the canyon wall and 94 species from the open margin. The species list showing the occurrence of each species in each habitat is shown in Table 2. The most speciose group was the teleostean fishes (61 species), followed by the crustaceans (47 species). Less abundant groups (non-crustacean invertebrates) included a few echinoderms: one asteroid, *Echinaster sepositus*, and one echinoid, *Brissopsis lyrifera* collected in the canyon head, and one species of holothurians, *Molpadia musculus*, sampled in the canyon wall and open margin. Molluscs were represented only by cephalopods (11 species). A single unidentified species of polychaete was recorded from the canyon head and wall sites.

Abundance and biomass

Table 3 shows abundance (A) and biomass (B) data for each phylum (Class for the Chordata) for each habitat and sampling month, as well as the total abundance and biomass for each sample and the mean total abundance and biomass (± standard deviation) for each faunal group. The mean total megafauna abundance grouped for each habitat was 8693 ± 4041 individuals·km^{-2} in the canyon head, 8872 ± 4528 individuals·km^{-2} in the canyon wall and 8685 ± 6609 individuals·km^{-2} in the open margin, with no significant differences of mean abundance between habitats (Kruskal–Wallis, *KS* = 0.461, 2 df, P > 0.1). The mean total megafauna biomass grouped for each habitat was 105 ± 50 kg·km^{-2} in the canyon head, 127 ± 34 kg·km^{-2} in the canyon wall and 108 ± 45 kg·km^{-2} in the open margin, with no significant differences of mean biomass between habitats (Kruskal–Wallis, *KS* = 0.854, 2 df, P > 0.1).

There was no clear inter-annual pattern of abundance and biomass for any faunal group (Table 3A, B) and therefore the data were pooled per habitat. Mean abundance and biomass of each faunal group was plotted per habitat (Fig. 2). There were no significant differences of total abundance and total biomass between habitats in any of the faunal groups (Kruskal–Wallis, 2 df, P > 0.1) excluding the annelids, which presented a significantly higher abundance (Kruskal–Wallis, *KS* = 15.213, 2 df, P < 0.005) and biomass (Kruskal–Wallis, *KS*=15.924, 2 df, P < 0.005) in the canyon head community. The faunal groups which accounted for most of the total abundance were the crustaceans, teleostean fishes and annelids (Fig. 2A, Table 3A). The faunal groups that contributed most to biomass were the crustaceans, teleostean fishes and chondrichthyans (Fig. 2B, Table 3B).

The contribution of individual species to total abundance and biomass varied between the three habitats. In the canyon head, the three most abundant species, accounting for 15% of the abundance, were the decapod crustaceans *Aristeus antennatus*, *Sergestes arcticus* and *Pasiphaea sivado.* In terms of biomass, *A. antennatus* and the fishes *Conger conger* and *Phycis blennoides* were the three species with higher biomass, accounting for over 30% of the total biomass. In the canyon wall, the crustaceans *A. antennatus* and *Plesionika martia* and the fish *Lepidion lepidion* were the three most abundant species (14% of total abundance), while *A. antennatus,* the fish *P. blennoides* and the chondrichthyan *Galeus melastomus* accounted for 36% of the biomass. Finally, in the open

Table 3 (A) (abundance, N·km^{-2}) and (B) (biomass, kg·km^{-2}) of megabenthos from the Blanes canyon and adjacent margin.

	April			May			August			September			December			March			April		Mean
	CH	CW	OM	CH	CW	OM	CH	CW	OM	CH	CW	OM	CH	CW	OM	CH	CW	OM	CW	OM	abund. ± SD
A																					
CNI	5.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5 ± 1.6
SIP	0.0	42.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.2	0.0	0.0	0.0	0.0	0.0	14.3	0.0	0.0	6.8	3.4 ± 9.8
ANN	217.6	63.2	0.0	1490.9	0.0	0.0	46.7	0.0	0.0	54.2	0.0	0.0	82.4	0.0	0.0	84.0	0.0	0.0	0.0	0.0	101.9 ± 331.3
CRU	12417.6	10610.5	10312.1	1981.8	2400.0	3054.7	3546.7	6950.0	3350.0	6445.8	3958.3	1924.1	7558.8	10028.6	18421.7	4680.0	4637.1	1741.7	1667.9	11124.7	6340 ± 4537.2
MOL	11.8	47.4	27.3	54.5	41.7	100.0	26.7	40.0	37.5	50.0	25.0	14.8	47.1	2.9	26.1	8.0	8.6	13.9	25.0	16.4	31.2 ± 22.9
ECH	11.8	36.8	0.0	0.0	4.2	1.9	0.0	0.0	4.2	12.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.5 ± 8.7
CON	270.6	84.2	184.8	36.4	45.8	71.7	80.0	30.0	95.8	83.3	62.5	51.9	182.4	14.3	17.4	16.0	102.9	75.0	171.4	31.5	85.4 ± 67.9
ACT	1700.0	5921.1	1930.3	1445.5	3579.2	1615.1	2046.7	3516.7	1695.8	2354.2	2675.0	1114.8	4470.6	1820.0	2067.4	636.0	2128.6	727.8	1350.0	943.8	2186.9 ± 1310.9
TOTAL	14635.3	16805.3	12454.5	5009.1	6070.8	4843.4	5746.7	10536.7	5183.3	9000.0	6720.8	3105.6	12341.2	11865.7	20532.6	5424.0	6891.4	2558.3	3214.3	12123.3	
B																					
CNI	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.02 ± 0.1
SIP	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.007 ± 0.0
ANN	0.1	0.0	0.0	1.6	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.1	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.09 ± 0.0
CRU	114.1	68.2	102.5	4.0	41.1	39.8	24.0	55.6	25.8	43.4	23.3	21.6	33.7	98.7	74.0	31.4	49.8	12.1	16.9	107.4	49.4 ± 33.8
MOL	0.3	5.7	8.1	0.8	5.8	3.4	2.4	3.5	17.9	1.6	2.8	0.3	1.6	0.1	6.8	1.3	1.3	0.6	2.0	2.8	3.4 ± 4.1
ECH	0.1	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.04 ± 0.09
CON	9.4	29.2	32.3	5.7	12.2	9.6	1.8	4.6	29.4	1.0	19.0	19.6	1.7	0.6	1.6	0.6	13.1	21.3	61.2	6.4	14.0 ± 15.2
ACT	30.4	46.6	31.6	22.7	131.5	21.1	112.1	59.2	81.1	73.3	49.2	28.4	96.8	25.0	11.1	15.7	34.3	26.0	27.9	15.9	47.0 ± 34.5
Total	154.5	150.1	174.6	34.7	190.6	73.9	140.3	122.9	154.2	119.7	94.3	70.0	133.8	124.4	93.4	49.1	98.6	59.9	108.0	132.5	

CNI = Cnidaria; SIP = Sipunculida; ANN = Annelida; CRU = Crustacea; MOL = Mollusca; ECH = Echinodermata; CON = Chondrichthya; ACT = Actinopterygii; Total = total abundance (A) and total biomass (B) per sample. CH = canyon head; CW = canyon wall; OM = open margin. Mean abun. = mean abundance per phylum; Mean biomass = mean biomass per phylum; SD = standard deviation.

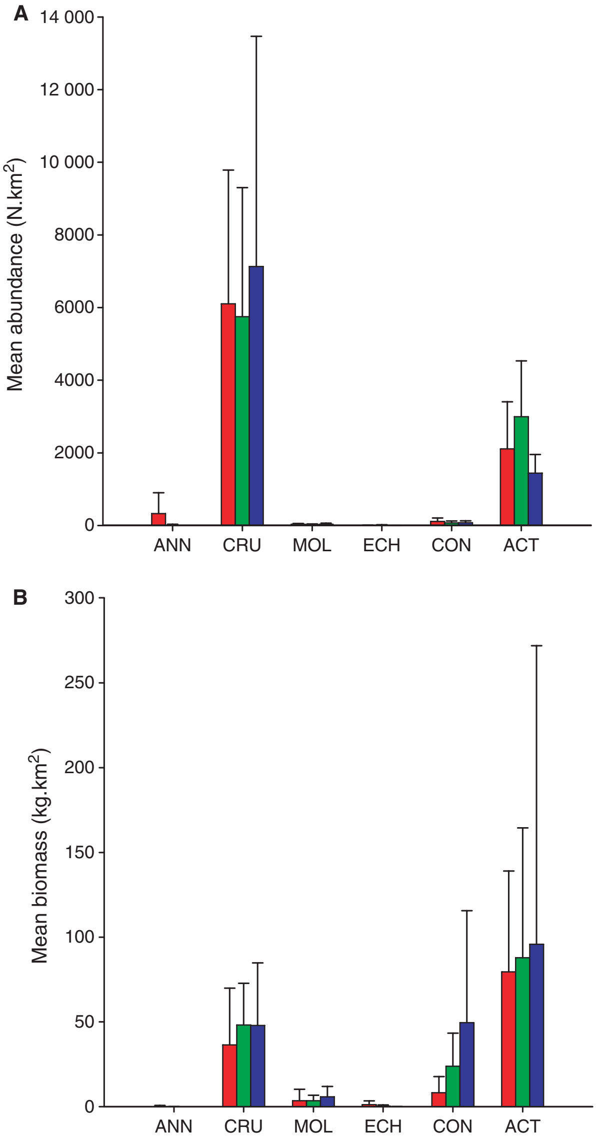

Fig. 2. Mean abundance ± standard deviation (A) and mean biomass ± standard deviation (B) of benthic megafauna from the Blanes canyon and adjacent margin, collected in the canyon head (red bars), canyon wall (green bars) and open margin (blue bars). ACT = Actinopterygia; ANN = Annelida; CON = Chondrichthya; CRU = Crustacea; ECH = Echinodermata; MOL = Mollusca. N = number of individuals.

margin, the crustaceans *A. antennatus* and *Pasiphaea multidentata* and the fish *L. lepidion* accounted for 17% of the total abundance, while *A. antennatus*, the chondrichthyan *G. melastomus* and the fish *Phycis blennoides* accounted for 38% of the biomass.

The mean individual weight of total fauna was significantly different between habitats (Kruskal–Wallis, *KS* = 9.896, 2 df, $P < 0.05$), increasing from the canyon head (28.5 ± 3.5 g·individual^{-1}) to canyon wall (59.0 ± 45.5 g·individual^{-1}) and open margin (82.5 ± 74.4 g·individual^{-1}).

Community structure and diversity

The structure of the different communities sampled presented some similarities related to habitat type and season. Cluster analyses of all samples (month × habitat) produced three primary groups (at 55% similarity) differentiating most samples per habitat (Fig. 3A). The first group includes all the margin samples (except one collected in winter 2003) and three samples from the canyon wall collected in spring. A second group includes most samples from the canyon head, the samples from the canyon wall collected in summer, autumn and winter and the sample collected in winter on the open margin. Finally, a third group includes three samples collected in spring in the canyon head and canyon wall. Within these clusters, pairs of samples are significantly similar (SIMPROF, $P < 0.05$) grouping within season (Fig. 3A). The MDS analysis of all samples indicated a trend that separates the open margin communities from the communities in the canyon head and canyon wall (Fig. 3B), with a transition of faunal community structure from the open margin to the canyon wall and onto the canyon head habitats. The analysis of community structure shows significant differences between habitats (canyon head, canyon wall and open margin) (ANOSIM, $R = 0.487$, $P < 0.05$).

The diversity indices varied between the open margin and the two canyon habitats. While the species accumulation curves from the canyon head and canyon wall are practically identical, the curve for the community from the open margin lies below (Fig. 4A). Similarly, mean Pielou's evenness (*J'*) and mean Shannon–Wiener diversity index (*H'*) were lower for the open margin community than for the canyon head and canyon wall communities (Fig. 4B,C) The k-dominance graph, which plots cumulative ranked abundance against species rank, shows the open margin curve above the canyon head and canyon wall, indicating a lower diversity in the open margin community (Fig. 5A). The computed ABC plots suggest that, of the three habitats studied, only the open margin community shows a moderate disturbance. In the community from the open margin, the abundance k-dominance curve lies above the biomass curve initially and then both curves largely intersect (Fig. 5D), suggesting a moderate to high disturbance for this habitat. In contrast, the ABC plots for the canyon head and canyon wall communities present the biomass curve above the abundance curve, suggesting undisturbed communities (Fig. 5B, C). These graphic results were confirmed by the W statistic, which was negative for the open margin ($W = -0.012$) and positive for

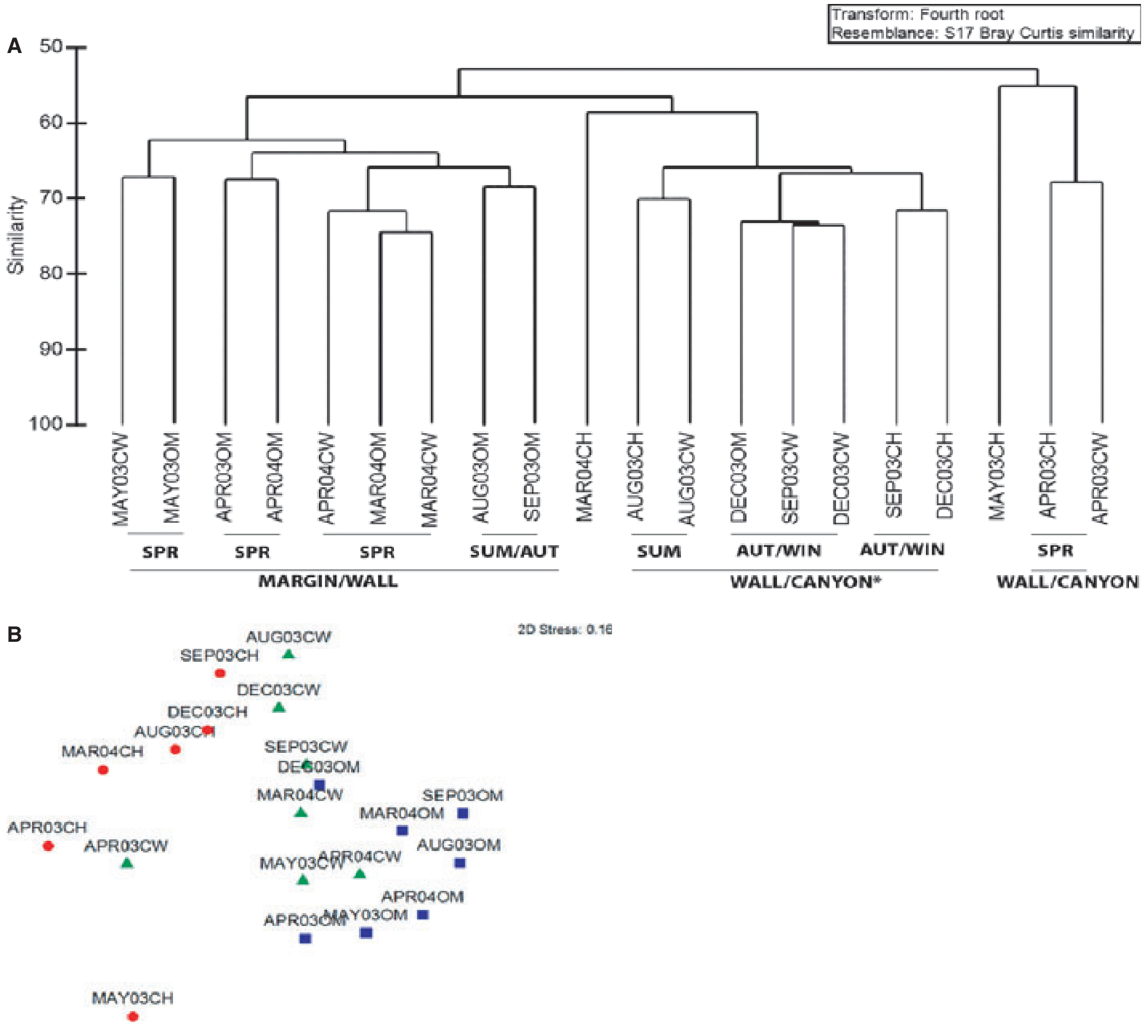

Fig. 3. Cluster analysis and SIMPROF test (A) and MDS analysis (B) on the abundance of benthic megafauna from the Blanes canyon and adjacent margin. Dashed lines on cluster indicates samples statistically similar (SIMPROF). SPR = spring; SUM = summer; AUT = autumn; WIN = winter; CH = canyon head; CW = canyon wall; OM = margin. Red circles = canyon head; green triangles = canyon wall; blue squares = open margin.

the canyon head (W = 0.06) and canyon wall (W = 0.092).

Discussion

While many deep-water Mediterranean studies have focused on abundance, biomass and distribution of the two most important bathyal groups, fishes and decapod crustaceans (Sardà *et al.* 1994a, 2004b; Stefanescu *et al.* 1994; Company *et al.* 2001, 2004; Puig *et al.* 2001; D'Onghia *et al.* 2004; Moranta *et al.* 2007), diversity analyses of deep-water communities for all megafaunal groups are still scarce (Fredj & Laubier 1985; Pérès 1985; Laubier & Emig 1993; Ramirez-Llodra *et al.* 2008; Sardà *et al.* 2009a). Our study provides, for the first time, a comprehensive species list of the benthic megafauna from the Blanes canyon and adjacent slope in the Northwestern Mediterranean. Teleostean fishes and decapod crustaceans were the most important groups, accounting for over 80% of the total biomass and abundance in all habitats, similar to what has been reported elsewhere for bathyal Mediterranean communities (see Sardà *et al.* 2004a and references therein). The number of megafaunal species (131) collected from the Blanes canyon and adjacent margin is considerably lower than that reported from the Merenguera canyon and adjacent slope on the margin off Barcelona, approximately 60 km south of Blanes (Sardà *et al.* 1994a; Ramirez-Llodra *et al.* 2008). When considering similar depths in both areas (450–650 m depth), 88 species of non-decapod crustacean invertebrates were

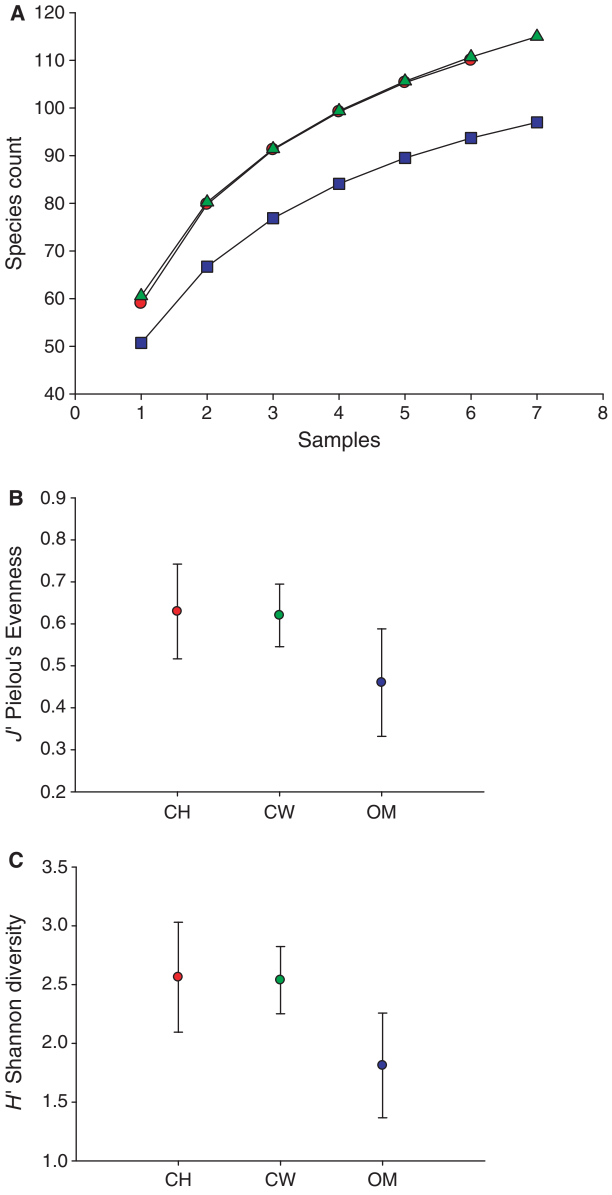

Fig. 4. Species accumulation plots (A), mean Pielou's evenness ± standard deviation (B), and Shannon–Wiener diversity ± standard deviation (C) for the communities in the canyon head (red), canyon wall (green) and open margin (blue).

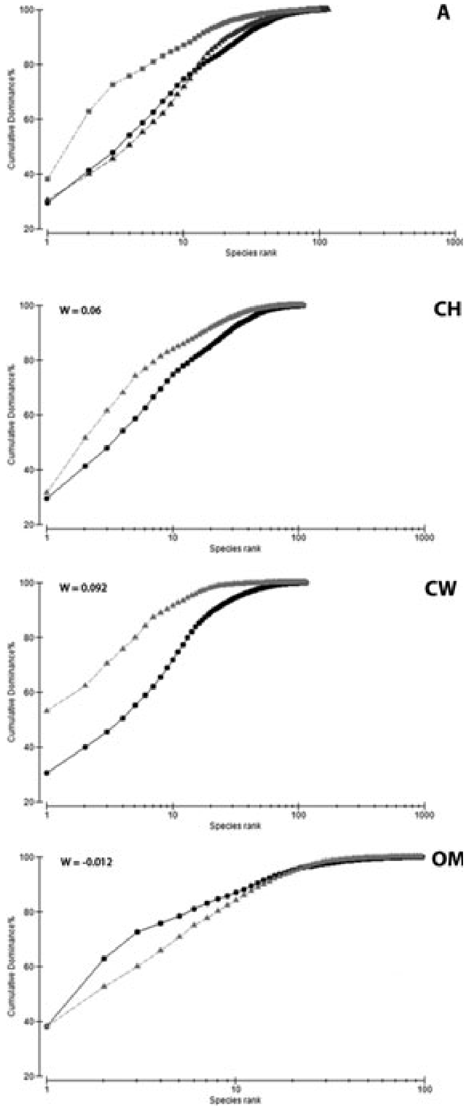

Fig. 5. K-dominance plot (A) for abundance of all megabenthic species from the Blanes canyon and adjacent margin: black circles = canyon head; dark grey triangles = canyon wall; Light grey squares = open margin. ABC plots for the communities from the canyon head (CH), canyon wall (CW) and open margin (OM). Black circles, abundance; grey triangles, biomass. W statistic: positive values expected for undisturbed conditions, negative values expected for disturbed conditions.

reported from the Merenguera area, sampled in 1991 and 1992 (Ramirez-Llodra *et al.* 2008), whereas only 24 species have been collected in the Blanes area. Community composition was also different between the two areas. In the Merenguera canyon and adjacent middle slope (450–650 m depth), the communities included large quantities of non-crustacean invertebrates, dominated by molluscs and echinoderms. Within the molluscs, Merenguera presented 13 species of gastropods (amongst which *Aporrhais serresianus* was very abundant), 24 species of bivalves and 13 species of cephalopods. Within the echinoderms, seven species of holothurians (*Molpadia musculus* being very abundant), two species of echinoids (amongst which *Brissopsis lyrifera* dominated), two species of ophiuroids and one species of asteroid were collected (Ramirez-Llodra *et al.* 2008). This faunal composition of the Merenguera canyon and slope differs substantially from the Blanes area where gastropods, bivalves and ophiuroids are absent and echinoderm abundance and diversity is much lower. The almost complete absence of these three faunal groups, which are in general epi- or endobenthic deposit feeders or scavengers, may be a result of sustained fishery activities over six decades in the Blanes area. ROV observations in the Blanes canyon in October 2007 (Company & Ramirez-Llodra, personal observation) have provided evidence of the physical damage on the sea floor caused by trawling gear, observed as deep tracks in the sediment. Therefore, it seems that continuous disturbance of the sea floor in the Blanes area represents a much higher impact on low motility burrowing species such as gastropods and echinoderms than on highly mobile species such as fish, decapod crustaceans and cephalopods, which are able to return to the disturbed zone from nearby non-fished areas. Different impacts of trawling on benthic communities have also been shown in an area subjected to a long-term fishery of *Nephrops norvegicus* in the Northeastern Irish Sea. Here, a significant negative effect of trawling on species richness, abundance and biomass of benthic infauna and epifauna was detected, whereas this effect was not found for the biomass of epibenthic fauna (Hinz *et al.* 2009). Also, the comparison of species composition and community structure between the middle (650 m) and lower (1200 m) slopes in the Merenguera showed a higher number of sessile filter feeders (sponges and cnidarians) and bivalves and gastropods in the lower slope. These results were explained by favourable environmental conditions (high currents and suspended organic material) related to the proximity of the canyon and by the lack of fishing pressure at 1200 m depth, which allows for the establishment and maintenance of sessile, delicate fauna (Ramirez-Llodra *et al.* 2008).

Several authors working on fish and decapod crustaceans have suggested a zonation of faunal assemblages on the Catalan margin (NW Mediterranean) related to hydrological characteristics, food availability, sediment type and changes in the steepness of slope (Abelló *et al.* 1988; Cartes & Sardà 1992; Cartes *et al.* 1994; D'Onghia *et al.* 2004). Four main assemblages are identified: shelf communities on terrigenous muds, upper-slope communities (250–400 m), mid-slope communities (400–800 m) and lower-slope communities (>1200 m), coinciding with the main zones described by Pérès (1985) for the Mediterranean deep-water fauna. The 400 m depth has been proposed as the boundary between the upper slope and the strictly bathyal fauna (Abelló *et al.* 1988). Our study sampled the mid-slope zone, where there were no significant differences in overall benthic megafauna abundance and biomass between canyon and the open margin habitats. The only group that varied in its abundance and biomass with habitat were the polychaetes, which showed a high relative abundance in the canyon head but not in the other two habitats. This is consistent with the higher abundance of polychaetes reported from the Merenguera canyon off Barcelona compared to the adjacent mid- and lower slope (Ramirez-Llodra *et al.* 2008). Previous studies in the Merenguera canyon and adjacent slope off Barcelona have shown that the abundance and biomass of fishes (Stefanescu *et al.* 1994), crustaceans and total megafauna (Sardà *et al.* 1994a) were higher in the canyon than on the adjacent margin at a comparable depth, attributed to higher food availability in the canyon. Similar patterns have been observed in the Hudson Canyon on the NE American margin (Rowe *et al.* 1982) and on the Portuguese margin (Gage *et al.* 1995). However, other studies have found either lower biomass in the canyon (Maurer *et al.* 1994) or no significant differences in the faunal biomass between the canyon and adjacent margin (Houston & Haedrich 1984). Whether there are differences in the abundance, biomass and species composition of macro- and megafauna inside and outside the canyon will depend on how different environmental and habitat factors, such as the disturbance regime in the canyon, the rate of organic matter deposition and the morphology of the canyon (Rowe *et al.* 1982; Vetter & Dayton 1999; Schlacher *et al.* 2007; Wei *et al.* in press), operate in each particular ecosystem (Levin & Gooday 2003). The lack of a 'canyon effect' promoting an increase in benthic megafauna abundance or biomass inside the Blanes canyon, contrasting with other Mediterranean canyons such as Merenguera, may be related to the long-term and intense fishing pressure over Blanes. Although both areas are exploited, the fishing intensity in the Merenguera canyon is lower than that of (Sardà *et al.* 1994a) the Blanes region, which has been subjected to year-round fishing for over 60 years for the rose shrimp *Aristeus antennatus* (Sardà *et al.* 2009b). Therefore, effects of chronic fishing pressure over bathyal benthic communities in the Blanes canyon and adjacent slope may limit the carrying capacity of the populations, keeping benthic megafauna biomass and abundance to levels not compatible with organically enriched systems such as a submarine canyon. A recent study of two large canyons in a heavily fished area on the Bering Sea has provided evidence of high biodiversity of megafauna, including corals and sponges, and of the significant damage caused by fishing lines (Morell 2009). Studies addressing fishing impact in canyons are still rare but necessary if we are to understand how anthropogenic pressure can contribute to margin heterogeneity and affect deep-sea communities in order to develop appropriate management options. This is particularly important in habitats such as canyons (Morell 2009) and seamounts (Clark & Rowden 2009), where hard substrata outcrops are often found colonised by sessile, slow-growing fauna, in some cases providing refuge or nursery areas for errant species, which are especially vulnerable to physical disturbance such as trawling or long-line fishing.

However, we did observe a 'canyon effect' on megabenthos community structure, in particular on biodiversity, in the Blanes region. The three diversity indexes measured were higher in the canyon samples (canyon head and wall) than in the open margin. Also, the k-dominance plots showed that canyon species were more evenly distributed. The groups that caused most of the difference between the canyon habitats and the open margin were polychaetes and several decapods and fishes that were only present in the two canyon sites, including the crabs *Philocheras echinulatus*, *Pagurus excavatus* and *Pagurus prideauxi*, the shrimp *Chlorotocus crassicornis*, *Plesionika edwardsii*, *Plesionika gigliolii* and *Plesionika heterocarpus*, and the fish *Capros aper*, *Lepidotrigla cavillone*, *Trigla lyra*, *Callionymus maculatus* and *Trachyrhyncus scabrus*. Higher non-crustacean invertebrate diversity in the canyon community in relation to the adjacent open margin has also been reported from the Merenguera canyon (Ramirez-Llodra *et al.* 2008). Benthic megafaunal biodiversity studies conducted to date in NW Mediterranean canyons have not addressed directly and in detail the relationship between physical (*e.g.* currents, sediment type) and ecological factors (*e.g.* food availability, competition) in shaping overall community structure patterns and distribution. However, according to several studies, the higher productivity and habitat heterogeneity of canyons contrasted to open margin environments leads to a higher benthic diversity in these particularly abrupt topography systems (Sardà *et al.* 1994a; Stefanescu *et al.* 1994; Vetter & Dayton 1999; Schlacher *et al.* 2007; Ramirez-Llodra *et al.* 2008). The community structure of the megabenthos in the Blanes margin also seems to be affected by the presence of the canyon, as shown in the MDS analyses. The community from the open margin formed a relatively well defined group, and a faunal transition from the margin to the canyon wall and to the canyon head is suggested. Within each large cluster (margin–canyon wall, canyon wall–canyon head), pairs of samples grouped seasonally, indicating that there are some variations in the community composition within the year, probably caused by movements of large mobile species such as decapod crustaceans, fishes and cephalopods. The differences in community structure observed in the open margin, which are not reflected in terms of abundance and biomass, could be explained by the higher fishing pressure on the margin habitat compared to the canyon sites (Sardà *et al.* 2009b). This was indeed suggested by the ABC plots, which indicate that while the canyon head and canyon wall are relatively undisturbed areas, the margin community, with its abundance curve above its biomass curve, presents signs of moderate to high disturbance.

A 'canyon effect' may also be reflected in the population structure of certain species. The overall individual size increased from canyon head to canyon wall and canyon margin. This has been reported in other studies for fish (Stefanescu *et al.* 1994) and crustacean decapods (Sardà *et al.* 1994b, 2003). Submarine canyons play an important role in the transfer of organic matter from the shelf to bathyal depths, which in some cases may be significantly higher than the organic matter input by passive sinking from the photosynthetic layers (Puig *et al.* 2000; Benthoux *et al.* 2002; Gage 2003; Canals *et al.* 2006; Company *et al.* 2008). It has been suggested that the higher food availability, together with a higher habitat heterogeneity in the canyon than on the margin, provides suitable conditions for recruitment of several species of fish and crustaceans (Sardà *et al.* 1994a,b, 2003; Stefanescu *et al.* 1994; Brodeur 2001; Tyler & Ramírez-Llodra 2002; Morell 2009), which could explain the overall smaller individual size found in the canyon sites on the Blanes area.

In conclusion, the Blanes canyon influences the community structure of the benthic megafauna, but this effect may be modulated by the anthropogenic pressure in terms of a benthic fishing industry that has been affecting this region for over 60 years. However, further dedicated studies investigating the effect of commercial bottom trawling on bathyal benthic communities are needed to confirm the observations made in the Blanes area and to fully understand the effects of fishing in habitats that often support high diversity and density of macro- and megafauna. Such studies are essential to provide critical information to policy makers and the fishing industry and to develop Ecosystem Approach to Fisheries management (Hiddink *et al.* 2006; Kaiser *et al.* 2006; Hinz *et al.* 2009; Sardà *et al.* 2009a).

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