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HABITATS AT THE MOROCCAN CARBONATE  
PROVINCE (GULF OF CADIZ, NE ATLANTIC)**

**BIODIVERSIDADE DA MACROFAUNA ASSOCIADA  
A HABITATS BATIAIS NA MARGEM MARROQUINA  
(GOLFO DE CÁDIS, NE ATLÂNTICO)**

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Dissertação apresentada à Universidade de Aveiro para cumprimento dos requisitos necessários à obtenção do grau de Mestre em Biologia Marinha, realizada sob a orientação científica da Professora Doutora Maria Marina Pais Ribeiro da Cunha, Professora Auxiliar do Departamento de Biologia da Universidade de Aveiro, e co-orientação da Doutora Clara Lúcia Ferreira Rodrigues, Investigadora em Pós-Doutoramento do Departamento de Biologia da Universidade de Aveiro.

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## palavras-chave

Mar profundo, corais de água fria, montes carbonatados, Escarpa de Pen Duick, vulcões de lama, macrofauna, biodiversidade, estrutura da comunidade

## resumo

O Golfo de Cádiz, localizado entre a margem sul Ibérica e a margem norte Marroquina, a oeste do Estreito de Gibraltar (NE Atlântico), engloba inúmeros montes carbonatados caracterizados pela acumulação de corais de profundidade fósseis e, mais de 40 vulcões de lama submarinos, a profundidades entre os 200 e 4000 m. Esta área localizada na interface de várias regiões biogeográficas, é tectonicamente ativa e caracterizada por uma longa história geológica; a complexa circulação de massas de água assegura a conectividade oceânica entre o Mar Mediterrâneo e as regiões Equatorial e Norte do Atlântico. No Golfo de Cádiz, a Escarpa de Pen Duick, com 4 km de comprimento e 100 m de altura, está situada a cerca de 500 m de profundidade no ramo sudeste do "Renard Ridge", na parte ocidental do campo de vulcões do El Arraiche.

Os corais de água fria, organismos vulneráveis e de crescimento lento que vivem em águas frias e escuras no oceano profundo, têm vindo a receber atenção acrescida nos últimos anos. No contexto dos programas de investigação MiCROSYSTEMS e Moundforce (Fundação Europeia para a Ciência), locais selecionados ao longo da margem Marroquina do Golfo de Cádiz foram investigados, com o objetivo de descrever a composição, abundância e estrutura das comunidades de macrofauna bentónicas que vivem em associação com habitats de recifes de corais de água fria predominantemente fósseis presentes nas proximidades de vulcões de lama e montes carbonatados.

A amostragem decorreu durante as campanhas M2005 (64PE237), M2006 (64PE253) e M2007 (64PE268), a bordo do NO *Pelagia*. Foram analisadas 120 subamostras de box-core recolhidas a profundidades entre os 220 e 900 m, nas quais foram identificados 426 taxa de macroinvertebrados. As comunidades de macrofauna revelaram ser altamente heterogêneas a nível de composição e estrutura, sendo maioritariamente representadas por artrópodes, anelídeos e moluscos. As análises multivariadas revelaram diferenças significativas entre estruturas geológicas distintas e entre diferentes tipos de substratos. Elevada biodiversidade, abundância e equitabilidade são comuns entre as comunidades de montes carbonatados, áreas coralinas e vulcões de lama, enquanto que nas zonas de referência ("off mound") e áreas sem presença de coral as comunidades de macroinvertebrados demonstraram ser caracterizadas por menor diversidade e abundância. No geral, estas comunidades são dominadas por uma percentagem relativamente baixa dos taxa mais comuns, incluindo principalmente poliquetas, sipúnculos e tanaidáceos. A análise em relação à profundidade também revelou diferenças a nível da riqueza de taxa e abundância.

Os resultados obtidos são discutidos em relação ao conhecimento prévio acerca da Escarpa de Pen Duick, montes carbonatados, recifes de coral fóssil, vulcões de lama da região de El Arraiche e área circundante, reforçando a hipótese de que a presença de montes carbonatados e recifes de coral de água fria fósseis aumentam a heterogeneidade de habitats no mar profundo e suportam uma comunidade de invertebrados bentónicos altamente diversa.

## keywords

Deep-sea, cold-water corals, carbonate mounds, Pen Duick Escarpment, mud volcanoes, macrofauna, biodiversity, community structure

## abstract

The Gulf of Cadiz is an extensive seepage area between the south Iberian and north Moroccan margins, west of the Strait of Gibraltar (NE Atlantic). It encompasses numerous carbonate mounds characterised by accumulations of mostly fossil deep-water corals, isolated coral patches and coral rubble, and over 40 submarine mud volcanoes at depths ranging 200 to 4,000m. This tectonically active area has a long geologic history and a central biogeographic location. The complex circulation of water masses ensures oceanographic connectivity with the Mediterranean Sea, Equatorial and North Atlantic regions. At the Gulf of Cadiz, the Pen Duick Escarpment, a feature with 4 km length and 100 m height, is located at ca. 500 m depth, on the south-eastern branch of the Renard Ridge, westwards of the El Arraiche mud volcano field.

Cold-water corals, vulnerable, slow-growing metazoans that inhabit cold dark waters in the deep-sea, have been receiving increased attention in recent years. Under the framework of the research programs MiCROSYSTEMS and Moundforce (European Science Foundation), selected sites along the Moroccan margin were investigated, aiming to describe the composition, abundance and community structure of the benthic macrofaunal assemblages living in association with fossil cold-water coral reef habitats present in the vicinity of mud volcanoes and carbonate mounds.

Sampling was undertaken during the cruises M2005 (64PE237), M2006 (64PE253) and M2007 (64PE268), onboard the RV *Pelagia*. From the 120 box-core subsamples collected at depths ranging 220 to 900 m, 426 macroinvertebrate taxa were identified. The macrofaunal assemblages were highly heterogeneous in composition and community structure and were mainly represented by arthropods, annelids and molluscs. Multivariate analyses supported significant differences between distinct geological features and between distinct substrate types. High diversity, abundance and evenness were common in mound, coral and mud volcano assemblages, whilst off mound sediments and areas without hard substrates were represented by less diverse and less abundant assemblages. The assemblages are dominated by a relatively low percentage of the most common taxa and include mainly polychaetes, sipunculids and tanaidaceans. Analysis in relation to depth also revealed differences in taxa richness and abundance.

The results obtained are discussed in relation to previous knowledge on carbonate mounds, fossil coral reefs, El Arraiche mud volcanoes and surrounding area, reinforcing the hypothesis that the presence of carbonate mounds and fossil cold-water coral reefs increases deep-sea habitat heterogeneity and support a highly diverse assemblage of benthic invertebrates.

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# 1. INTRODUCTION

## 1.1. The deep sea and the cold-water coral ecosystems

The deep-sea (>200 m) is often viewed as a huge, dark, and inhospitable place that represents the largest portion of the ocean; waters deeper than 1,000 m cover an estimated 62% of the planet. This undiscovered world constitutes one of the last great wildernesses on Earth: through the early 20<sup>th</sup> century knowledge on the marine realm was mostly confined to a small number of intellectual curiosity seekers and deep-sea explorers. Therefore, the deep ocean constitutes the most poorly sampled habitat on Earth and patterns of diversity and distribution of the majority of species remain largely unresolved (Yesson *et al.*, 2012). In spite of more than 150 years of exploration, the ocean depths remain virtually unknown due to the technological challenges and financial resources required to explore this environment. However, decreasing opportunities in coastal waters led industries to explore the deep ocean for new resources: deep-water fisheries developed, petrochemical industries moved deeper into continental slope waters, and mineral extraction from deep-ocean sites became feasible (Roberts, 2002).

Biological science has so far touched upon only one millionth of the deep-sea floor, but, with improved deep-water technology and societal interest, our knowledge of the deep-sea grew considerably during the past decades. Science discovered that habitats previously considered devoid of life were areas of high biodiversity; new underwater technology revealed remarkable new and exotic habitats such as exuberant hydrothermal vents, cold seeps, gas hydrates, massive sulphide deposits and cold-water coral reefs, which harbour diverse and unique faunas. One of the most spectacular events in the investigation of the European continental margin during the last decade has been the discovery of the giant carbonate mounds along the Celtic margin; in depths of 700-1,000 m, these up to 300 m high carbonate build-ups composed of cold-water coral fragments embedded in a loose matrix of hemipelagic sediments are covered by extensive coral reefs (Wehrmann *et al.*, 2011).

Cold-water coral mounds and reefs are large areas of coral accumulation; these biogenic features have been known to occur in the deep-sea for centuries, firstly attracting the attention of only local fishermen and a small global community of biologists and geologists. Although their existence was first documented over 250 years ago, it was only in the 1990s that research on these ecosystems received a new impetus (Freiwald *et al.* 2004; Wienberg *et al.*, 2009). Recently, with the development of increasingly sophisticated and efficient modern technologies, such as manned and remote operated submersibles, advanced acoustics survey techniques, sonar, bottom landers, mini-submarines, and production of high quality images by underwater video photography, scientists around the globe have finally been able to explore, study and map deep-sea coral communities in their natural environment (Roberts and Hirshfield, 2004; Roberts *et al.*,

2006; Turley *et al.*, 2007). Astonishing images of deep-sea corals living at depths from surface down to more than 1,000 m are now available, and have led many countries to initiate the assessment of the distribution, status, health, ecology, and potential threats faced by these ecosystems (Freiwald and Roberts, 2005; Hall-Spencer *et al.*, 2002; *Lophelia*, 2012; Roberts, 2002).

Cold-water coral ecosystems are emerging as systems of ecological and economic value, raising concern over their rapid destruction. The structural complexity of these ecosystems harbours a yet unknown number of different species, including large numbers of commercially important fish species. Therefore, deep-sea corals (as well as sponge aggregations) appear to be important biodiversity hotspots in the oceans and provide vital resources for fisheries, bioprospecting, science and education (Baillon *et al.*, 2012; Hain and Corcoran, 2004; WWF, 2004). In addition, benefits to humans derived from deep-sea corals such as direct goods and services are just beginning to be explored: marine natural products constitute a diverse group of biomedically important compounds that gave a new impetus to the search for bioactive substances produced by living organisms and useful genes. Cold-water Cnidaria and Porifera were, historically, among the first marine animals to be chemically studied and constitute a largely untapped resource of natural products with enormous potential as pharmaceuticals, nutritional supplements, enzymes, pesticides, cosmetics, and other commercial products (Freiwald *et al.*, 2004; Lebar *et al.*, 2007; Roberts and Hirshfield, 2004).

Due to their longevity over geological time scales, cosmopolitan distributions, and banded skeletal structure, some deep-sea corals can also serve as important paleoenvironmental archives. They reflect temporal variations of past climate variables, such as sea surface temperature, salinity or productivity, that are fundamental in reconstructing climate history and understanding global climate change (Roberts *et al.*, 2006; Witherell and Coon, 2001). However, there is still a paucity of information on the basic biology, ecology, abundance and distribution of the numerous species of deep-water corals found in all the world's oceans, because most of them are largely hidden, ignored, and not easily accessible, and thus, difficult to map and sample (Freiwald and Roberts, 2005; Hain and Corcoran, 2004; Kellogg *et al.*, 2009; Thiem *et al.*, 2006).

## **1.2. Cold-water corals: fragile havens in the deep**

While most people are aware of tropical corals, few are aware that two-thirds of all known coral species inhabit cold dark waters in the deep oceans. The terms "deep-sea coral", "cold-" or "deep-water coral" have all been used to discriminate these coral frameworks from the famous coral reefs of shallow, warm-water tropical seas (Cairns, 2007; Freiwald and Roberts, 2005; Rogers, 2004). Unlike tropical corals, the majority of deep-water reef-forming corals are not associated with zooxanthellae (i.e. symbiotic dinoflagellates); therefore, they are termed azooxanthellate (Maier *et al.*, 2009; Turley *et al.*, 2007; Wheeler *et al.*, 2007). Deep-sea corals show great diversity in size, shape, and colour; some are stony and stiff, while others are soft and

sway with the ocean currents. Some of these construct unexpectedly vast banks, reef structures or giant carbonate mounds, measuring several meters in height and tens of kilometers in length (e.g. Norwegian coast); however, most do not build reefs, but instead smaller scattered and isolated colonies with no more than a few meters in diameter, on small biological topographic build-ups, and others are solitary individuals (Freiwald *et al.*, 2004; Hain and Corcoran, 2004; Roberts and Hirshfield, 2004; Roberts *et al.*, 2006; WWF, 2004).

Across the world, over 4,200 species of cold-water corals have been recorded by scientists. Reef-building and habitat-forming corals in cold waters are derived from several taxonomic groups belonging to the phylum Cnidaria. Corals belonging to the class Anthozoa ("true corals") can be further divided into the subclasses Hexacorallia and Octocorallia (soft corals); hexacorals include the order Scleractinia (the colonial "stony corals", that constitute the focus of this study) which build the hard, calcium-based reefs most commonly associated with corals (Freiwald *et al.*, 2004; Lindner *et al.*, 2008; Roberts *et al.*, 2006; Roberts and Hirshfield, 2004; WWF, 2004). The most widespread and best-studied stony coral is *Lophelia pertusa*, an azooxanthellate, colonial cold-water coral that was first described from the North-East Atlantic in the mid-18th century by Linnaeus (1758). The name *Lophelia* derives from the Greek "*lophos*" and "*helios*", meaning 'a tuft of suns', referring to the individual sun-like coral polyps, evident in **Figure 1** (*Lophelia*, 2012; Roberts *et al.*, 2003). Its robust skeletons form massive, highly branched bush-like colonies that can measure few centimeters to several meters across, consisting of many thousands of translucent coral polyps. As the colony develops, adjacent branches tend to fuse, thereby considerably strengthening the architectural stability of the entire framework (De Mol *et al.*, 2002; Masson *et al.*, 2003; Reed, 2002).

Deep-water corals have lower growth rates and longer lifespans than the majority of shallow water corals. Deep-sea reefs take thousands of years to develop and the geological records show that these reefs have existed for millions of years (Turley *et al.*, 2007; Witherell and Coon, 2001). The rate of linear extension of branches of the deep-water scleractinian coral *Lophelia pertusa* varies between 1-26 mm per year and the growth rate of a *Lophelia* reef is estimated to be 1.3 mm per year, meaning that reefs where the framework thickness is tens of meters thick are thousands or even tens of thousands of years old. Consequently, it will take hundreds of years for a colony to reach a diameter of 1.5-2 m while it will take thousands of years to build a reef structure 10-30 m thick. A 1.5 m high colony of *L. pertusa* may be up to 366 years of age. Therefore, while individual corals may live only for a few decades or centuries, cold-water coral reefs can be very old. Radiocarbon dating of *L. pertusa* from the Sula Ridge reef off Norway (the second largest known in the North-Eastern Atlantic) suggests that it has been growing for around 8,600 years, while reefs off the west of Ireland are at least 1.8 to 2 million years old (Fosså *et al.*, 2002; Freiwald *et al.*, 2004; Freiwald and Roberts, 2005; Hain and Corcoran, 2004; Mortensen *et al.*, 2001; Rogers, 2004).

Over time, continual coral growth can produce large reef structures often dominated by *Lophelia pertusa* but also containing other secondary framework-constructing Scleractinia (Davies *et al.*, 2008; Roberts *et al.*, 2005). Like *Lophelia* sp., corals of the *Madrepora* group are cosmopolitan, and occur in the same environments. *Madrepora oculata* (**Figure 1**) forms branched colonies with a maximum of only 30-50 cm high, which are generally much more fragile and tend to break off easily, thus considerably limiting their capacity to build large frameworks or reefs. *Madrepora* usually colonises dead and broken *Lophelia* colonies (De Mol *et. al.*, 2002; Freiwald and Roberts, 2005; Freiwald and Wilson, 1998; Hansson *et al.*, 2009). These species are often associated with the solitary stony coral *Desmophyllum dianthus* (Esper, 1974) recently discovered at just 20 m depth in Chilean fjords, *Goniocorella dumosa* (Alcock, 1902) that builds conical-shaped reefs, *Solenosmilia variabilis* (Duncan, 1873) which produces tightly-branched reef frameworks, *Enallopsammia profunda* (Pourtalès, 1867) that form massive dendroid colonies up to 1 m thick, and *Oculina varicosa* (Lesueur, 1821), the “ivory tree coral”, a species quite unusual because it can occur in both shallow and deep waters (De Haas *et al.*, 2009; Frank *et al.*, 2009; Freiwald *et al.*, 2004; Hain and Corcoran, 2004; Rogers, 2004).



**Figure 1.** *Lophelia pertusa* (left) and close-up of *Madrepora oculata* (right). © Diana Catarino, UAzores. From Hermione (2012).

There is evidence that *Lophelia pertusa* is capable of catching live prey, feeding primarily on live zooplankton of up to 2 cm that drift past the coral framework on currents (eg. calanoid copepods, semi-pelagic crustaceans such as swimming cumaceans and chaetognaths); the polyps are also capable of taking relatively large prey items such as euphausiids. This species appears to be an opportunistic feeder, taking any available nutritious particle; it also feeds on bacteria, protozoans, phytoplankton and flesh particles from different types of marine animals such as fish and mussels (Freiwald *et al.*, 2004; Hain and Corcoran, 2004; Mortensen *et al.*, 2001; Roberts *et al.*, 2006; Rogers, 2004). Zooplankton is also a nutritional source for *Desmophyllum dianthus*, importantly sustaining respiratory metabolism, growth and organic matter release, with further

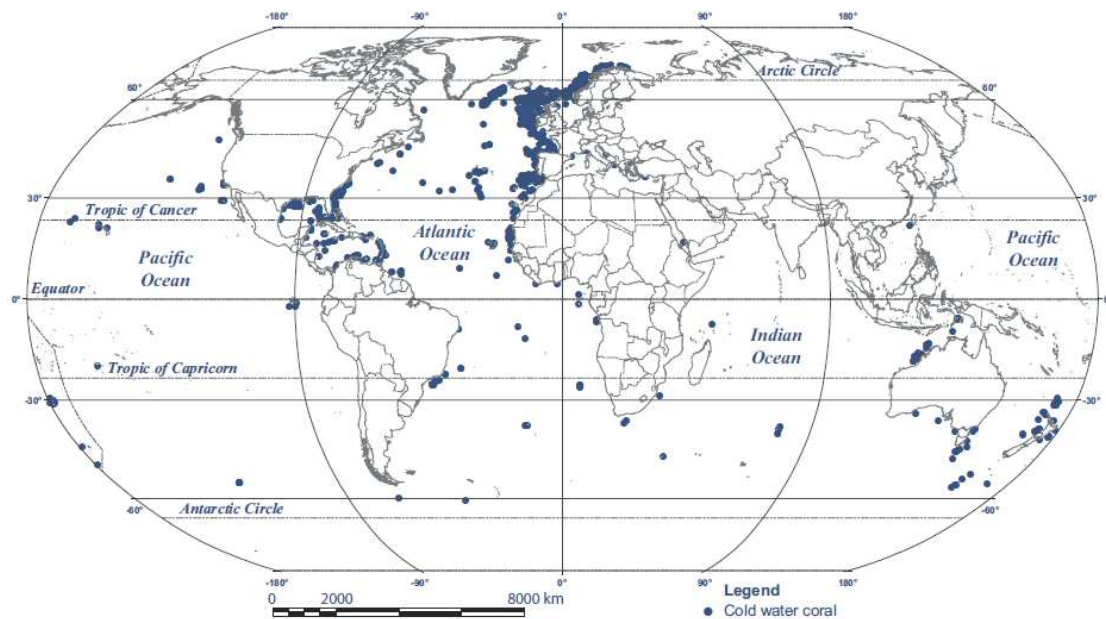
implications for the role of cold-water corals as deep-sea reef ecosystem engineers (Naumann, *et al.*, 2011). Such observations suggest that cold-water corals can have a varied diet and not specialized to one kind of animal food, relying on a food chain supported by high primary surface production. Besides, it has been recognized that bacteria are an important part of their biology, as they play a significant role in the nutrition of their host, influencing its health and distribution (Hansson, *et al.*, 2009; Kellogg *et al.*, 2009; Roberts *et al.*, 2003).

Present knowledge of deep-water coral reefs distribution is incomplete and is largely based on historic data and on detailed studies of a few species in limited geographic areas; lack of funding and expertise has left large oceanic areas unmapped, potentially hosting unknown reefs (Roberts *et al.*, 2005; WWF, 2004). Despite this, some intriguing patterns in their global biogeography are becoming evident (Roberts *et al.*, 2006). Cold-water coral reefs have been reported in many regions, where they produce complex three-dimensional reef frameworks, but the fairly precise environmental requirements of these organisms mean that they can only form reefs in specific localities (Freiwald *et al.*, 2004; Rogers, 2004).

Cold-water corals are commonly found on the continental margins in a wide range of depth and latitude (**Figure 2**) (see review in Braga-Henriques, 2013); to date, most studies have been carried out at high latitudes, where cold-water coral communities have been mainly reported from the photic zone to abyssal depths (from 200 to 6,000 m) on the continental shelf and slope (Roberts *et al.*, 2006; Thiem *et al.*, 2006). The outcomes of several research projects over the past 20 years demonstrated that some of these coral species are ubiquitous in the world oceans, but are not known from most of the Arctic Ocean, and others are restricted to only a few locations or even a single place (Cairns, 2007; Roberts and Hirshfield, 2004; Wienberg *et al.*, 2009). They have been recorded along the cold-temperate Northeast European Atlantic continental margins and in the South-West Ireland, Scotland and Iberian margin (Azores, Madeira and Canary Islands). There are also records from the Mediterranean Sea, Gulf of Cadiz, Senegal and the Cape Verde Islands in West Africa, and in the Western North and South Atlantic (from Nova Scotia and the United States, to the Gulf of Mexico and Brazil). A small number of non-reef records from the Indian and eastern Pacific Oceans was also registered (Freiwald *et al.*, 2004; Freiwald and Roberts, 2005; Hain and Corcoran, 2004; Pirlet *et al.*, 2010; Reed, 2002).

In the North Atlantic and the Mediterranean Sea *Lophelia pertusa* and *Madrepora oculata* are the most abundant reef builders. While the first is usually found in water depths of than 2,000 m, *M. oculata* occurs with a depth range of ca. 50 to over 1,500 m (De Mol *et al.*, 2002; Hansson, *et al.*, 2009; Reed, 2002). The shallowest records of *Lophelia* reefs are in the Norwegian fjords where they have been observed at just 39 m depth on the Tautra Ridge, mid-Trondheimsfjorden and in the New Zealand fjords, due to special conditions that exist in these environments, while the deepest records extend down to 2,775 m in Morocco and to 3,383 m at the New England seamount chain in the North Atlantic (Fosså *et al.*, 2002; Mortensen *et al.*, 2001). The world's

largest cold-water coral reef known so far is the Røst reef, southwest of Lofoten Archipelago, northern Norway, which was discovered in 2002. This reef lies in 300-400 m depth, is 43 km long and 2-3 km wide, covering an area of 100 km<sup>2</sup>, and is primarily built by *L. pertusa* (Freiwald *et al.*, 2004; Freiwald and Roberts, 2005; Hain and Corcoran, 2004; Rogers, 2004; WWF, 2004). It is much larger than the previously largest known reef in water depths of 270 to 310 m at 64°N on the Sula Ridge, off the Norwegian west coast, with approximately 13 km long, 300 m wide and up to 35 m high. These and other Norwegian reefs have the highest densities of *L. pertusa* corals (Gass and Roberts, 2006; Masson *et al.*, 2003; Roberts and Hirshfield, 2004; Thiem *et al.*, 2006).



**Figure 2.** Global distribution of cold-water corals: blue points on the map indicate coral reef records around the world, of varying size and stages of development, but not the actual area covered. This map should be regarded as a conservative compilation of locations, as more reefs are being discovered each year. The high density of reefs shown in the North Atlantic most probably reflects the intensity of research in this region. From Hain and Corcoran (2004).

Almost all known coral ecosystems share a number of special environmental requirements that control their distribution and growth, such as a suitable hard surface on which to attach (e.g. rock, shells, dead coral framework, glacial boulders, gravel or pebble) (De Haas, *et al.*, 2009; Gass and Roberts, 2006; Masson *et al.*, 2003; Rogers, 2004). These corals live typically in areas with stable physical conditions, under a restricted temperature range recorded between 4 and 14°C, and only occur in waters with salinity values from as low as 32.0 psu in Scandinavian fjords to at least 38.8 psu in the Ionian Sea). Several lines of evidence suggest that ambient oxygen level may also be an important factor in controlling the distribution of these animals in the



ocean (Freiwald *et al.*, 2004; Freiwald and Roberts, 2005; Hain and Corcoran, 2004; Mienis *et al.*, 2007; Roberts *et al.*, 2003; Wheeler *et al.*, 2007).

Scleractinian corals require an adequate nutrient supply and protection against burial to grow; they are frequently reported in high concentrations from regions where current-seabed topography interactions (e.g. topographic elevations or flow constrictions) generate increased flow velocities close to the seabed (De Mol *et al.*, 2002; Freiwald and Roberts, 2005; Masson *et al.*, 2003). As sessile filter feeders, cold-water corals must rely on currents to supply food for nourishment; therefore, they appear to grow preferentially in turbulent hydrodynamic environments with high productivity. Nutrient-rich waters stimulate the development of high phytoplankton and zooplankton levels, providing a major food source for the coral communities and other suspension-feeding organisms (Hain and Corcoran, 2004; Reed, 2002; Thiem *et al.*, 2006). Consequently, they prefer fairly strong and fast directional bottom currents that prevent deposition of sediments and smothering the developing corals and associated fauna, remove waste products, and also keep organic matter in suspension (Davies *et al.*, 2008; Frank *et al.*, 2009; Mienis, *et al.*, 2009; Mortensen *et al.*, 2001; Wheeler *et al.*, 2007; Wienberg *et al.*, 2009).

According to this, one of the most decisive factors that control their location appears to be the seabed topography. Most observations of cold-water corals have been, in areas with accelerated currents, such as on sloping and irregular topography and topographic highs of various scales that form obstacles in the current path with more prolific growth occurring on exposed flanks and summits (Davies *et al.*, 2008; Mortensen *et al.*, 2001; Wheeler *et al.*, 2007). Scientific expeditions have found that seamounts, outcropping hardrock, sedimentary and carbonate mounds, offshore ridges, deep-sea canyons and flanks of oceanic banks are all favourite places for *Lophelia* to grow (Hain and Corcoran, 2004; Rogers, 2004; Thiem *et al.*, 2006).

### **1.3. Habitat complexity of cold-water corals**

Once a small coral colony has settled and the mentioned favorable environmental conditions are fulfilled over an extensive period, these organisms can form important carbonate mound structures which persist in the geological records. They produce complex, but extremely fragile three-dimensional frameworks and the colony expands, providing a multitude of micro-niches for a highly diverse reef-associated community (De Mol *et al.*, 2002; Freiwald *et al.*, 2004; Maignien *et al.*, 2011). Cold-water corals are thus considered as important structural components of benthic habitats, potentially enhancing local abundance in a variety of fish and invertebrate species (Braga-Henriques, 2013; Yesson *et al.*, 2012). Deep-water coral colonies have a complex architecture, providing sheltered cavities which often contain organic rich sediments, while the outer parts provide a high water flow with little sedimentation. These biogenic structures also provide a low-disturbance environment in which the fauna is protected against physical erosion and predation. Therefore, deep-sea corals, sponges, and other habitat-forming organisms may

function as feeding, shelter, refuge, breeding, spawning, and/or nursery habitats for numerous species (Freiwald and Roberts, 2005; Roberts and Hirshfield, 2004; Turley *et al.*, 2007). Besides, recent geophysical studies have demonstrated that several species of cold-water corals are significant autogenic ecological bio-engineers able to build large reef frameworks (termed "bioherms") in the aphotic zone; these structures provide an important substrate and suitable habitat, forming an essential environment for growth and further development of corals and other suspension feeding organisms (Davies *et al.*, 2008; Davies *et al.*, 2011; De Haas, *et al.*, 2009; Masson *et al.*, 2003; Mienis, *et al.*, 2009; Rogers, 2004).

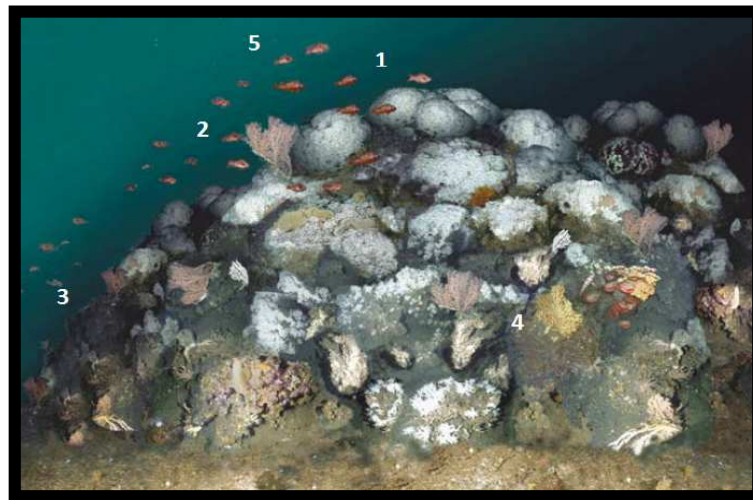
Cold-water coral mounds vary in size and shape ranging from small, low relief ovoid features, to giant mounds, conical to ridge and ring-shaped features, and in some cases having very steep sides. This morphological variation is an expression of the influence of differing environmental controls (e.g. current dynamics, temperature, salinity, pH, organic particulate supply, etc.) on mound formation and growth. A typical mature cold-water coral reef structure passes through several evolutionary stages and several mound growth models have been proposed to explain their formation, growth and development (Freiwald *et al.*, 2004; Mienis, *et al.*, 2009; Wheeler *et al.*, 2007). The availability of suitable hard substrate on the seabed is an essential pre-requisite for the settling of coral larvae. If the environmental conditions are suitable, coral colonies can expand themselves across areas of soft sediment either by sexual reproduction or by branch fragmentation and re-growth, until they become unstable and eventually older portions of the branches break (Reed, 2002; Roberts *et al.*, 2003; Roberts *et al.*, 2006). Upon death of the corals, subsequent coral generations use their predecessors and other carbonate debris produced by associated benthic fauna as a substrate to settle, stimulating renewed growth and further re-colonization around the initial colony. Once the mounds reach a certain height above the surrounding seabed they influence the currents around them and a positive feedback mechanism will evolve: vertical growth of corals results in the formation of mounds with steep slopes, which in turn results in increased currents supplying additional food for the corals, enhancing coral growth and thus mound formation, which strengthen the local currents, etc. (De Haas, *et al.*, 2009). A final mature phase may result in which the mantle of living coral is relatively negligible to the large volume of dead coral. Due to this, corals grow preferentially in elevated positions where they can take advantage of faster flowing waters delivering organic particulate food supply, and avoid the higher concentration of inorganic sediment closer to the benthic boundary layer (Freiwald and Roberts, 2005; Reed, 2002).

Coral fragments are the result of a bioerosion process that starts with the death of coral colonies due to persistent attack by boring organisms such as clionid sponges, worms, foraminiferans, fungi, bryozoans and phoronid worms to the older region of each colony. This eroded debris disintegrates due to chemical dissolution (biocorrosion) and mechanical breakup of the coral aragonite (bioabrasion) (Freiwald *et al.*, 2004). Skeletal loss of 70-80% of the thickly calcified coral skeletons due to locally intense sponge excavation results in the weakening of the

stability and in the eventual collapse of the coral constructions onto the sediment floor (De Haas, *et al.*, 2009; Reed, 2002; Rogers, 2004). Because of the dynamic origin of the habitat between living corals and coral rubble, it is referred to as a “coral degradation zone” (Raes and Vanreusel, 2006). In a final stage of the degradation process, intensified bioerosion and less stabilizing sponge encrustation will result in accumulations of cm- to dm-sized coral debris or rubble. These rubble “graveyards” not only act as sediment trap but also as micro-habitat for a wide range of organisms (Freiwald and Wilson, 1998; Freiwald and Roberts, 2005; Van Rooij *et al.*, 2011).

#### 1.4. Cold-water coral associated assemblages

According to Freiwald *et al.* (2004) model, a cold-water bioherm can be divided into two major habitats: a central living coral zone on the summit and the upper flanks (**Figure 3.1**), overlying a lower framework zone of dead coral and sponge skeletons (e.g. *Aphrocallistes beatrix*) mixed with sediments (**Figure 3.3**). A transition of dead coral at the base of the mounds gives way to denser live coral coverage (**Figure 4**) progressing upwards on the mound (De Mol *et al.*, 2002; Freiwald and Roberts, 2005; Rogers, 2004).



**Figure 3.** Model of a *Lophelia*-reef. **1)** On the top of the reef the hemispherical living colonies are found. **2)** Below this zone living colonies of varying size are found with dead corals in between. **3)** At the base there is a zone characterised by smaller fragments of coral (rubble) mixed with sand and mud. **4)** *Paragorgia arborea* and other gorgonians are common on the reefs. **5)** *Sebastes* spp. are often seen in considerable numbers in connection with the reefs. The reef is about 10 m across. Modified from Freiwald *et al.* (2004).

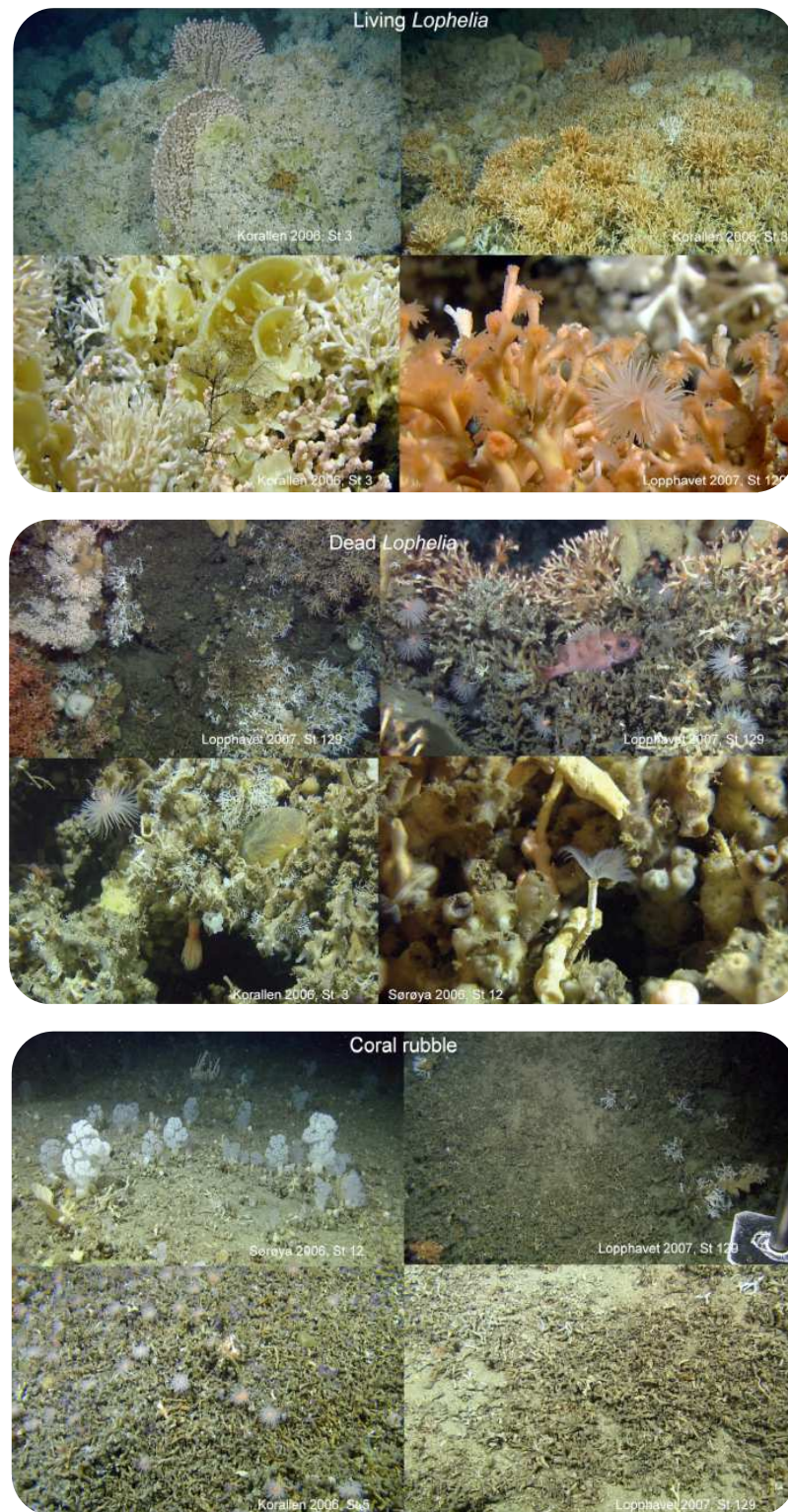
The development of a biofilm, associated with selective Fe-Mn precipitation on the coral skeleton might enable an entirely new food web as a food source for meiofauna and higher trophic levels (macro- and megafauna), with higher diversity in the living or dead coral

framework. However, living coral is not a suitable substrate for this fauna because it responds to the settlement of sessile organisms by an increase in mucus production in areas of infestation and is able to encrust repetitively attached organisms by precipitation of selectively secreted sclerenchyme layers, resulting in the thickening of the skeleton (Freiwald and Wilson, 1998; Freiwald and Roberts, 2005).

Studies on associated fauna of deep-sea cold-water corals have shown that their biodiversity is comparable to that of tropical coral reefs. Deep-sea corals have been shown to be associated with high abundances of rich fish and invertebrate communities (Baillon *et al.*, 2012; Freiwald *et al.*, 2004) (**Figure 5**): *Lophelia pertusa* is known to support over 1,300 species of associated fauna in the NE Atlantic and *Oculina varicosa* was found to be a feeding, spawning and shelter habitat for many commercially and recreationally important fish species, including the gag grouper (*Mycteroperca microlepis*) and scamp grouper (*Mycteroperca phenax*), the greater amberjack (*Seriola dumerili*), and juvenile speckled hind (*Epinephelus drummondhayi*) (Hain and Corcoran, 2004; Rogers, 2004).

These reefs appear to offer a critical complex habitat to many species of fishes, in areas that lack defined topography. Underwater video observations of *Lophelia* reefs from the Sula Ridge off Norway recorded fish species such as redfish (*Sebastes marinus*), saithe (*Pollachius virens*), ling (*Molva molva*), tusk (*Brosme brosme*) and pregnant Norway redfish (*Sebastes viviparus*), that also were larger and more abundant around deep-sea corals. Therefore these reefs create a multitude of ecological niches, which provide firm substrata and favor the settlement and growth of many invertebrates; more than 980 invertebrate species are known to be associated with these corals, belonging to a broad range of taxa: Foraminifera, Cnidaria (hydroids, octocorals, sea anemones), Porifera (sponges), Annelida (polychaetes), Arthropoda (decapods, isopods, amphipods, cirripeds, etc.), Mollusca (bivalves, gastropods), Echinodermata (asteroids, echinoids, ophiuroids, crinoids), Bryozoa, Chordata (ascidians), Brachiopoda, Nematoda, Sipuncula and Nemertea (De Haas, *et al.*, 2009; Freiwald *et al.*, 2004; Freiwald and Roberts, 2005; Hain and Corcoran, 2004; Hall-Spencer *et al.*, 2002; Reed, 2002; Roberts and Hirshfield, 2004). Although most of these organisms are not found exclusively on *Lophelia* banks, sharply demarcated from the surrounding seabed, many of them are much less common outside of the reef and distinct from the background deep-sea fauna (Rogers, 2004).

While large mobile predators and economically important organisms live amongst the coral branches, seeking protection (fish, shrimps, lobsters, and crabs), other organisms live mainly attached to dead coral framework or rubble (other corals, sponges, anemones, clams, crinoids, ophiuroids, sea urchins), so they may better filter food from the currents. Sponges and worms can live within cavities inside the dead coral branches or within the sediments around the reefs, and other animals, such as sea stars, snails, gastropods and crustaceans feed directly on the corals tissues (Freiwald and Roberts, 2005; Roberts and Hirshfield, 2004; Rogers, 2004).



**Figure 4.** Impressions of the live and dead *Lophelia* habitat and coral rubble habitat, from reefs off northern Norway (from the top to the bottom, respectively). From Hermione (2012; Deliverable 4.9).



**Figure 5.** Examples of marine species associated to cold-water corals. **A)** School of young *Paromola cuvieri* guarded by an adult (Gulf of Cadiz, Moroccan margin); **B)** *Helicolenus dactylopterus* (Blackbelly rosefish); **C)** Egg capsules containing living embryos of the oviparous deep-water blackmouth catshark *Galeus melastomus* found tightly nested in living *Lophelia* colony framework on the Mingulay reef complex (July 2009 and 2011). From Hermione (2012).

This fauna, however, is difficult to sample and not all sub-habitats in *Lophelia* reefs have been investigated to date; the species richness, biodiversity and ecological importance are still unknown (Hain and Corcoran, 2004). The ecological role of deep-water corals in providing habitat structure for fish and other marine life, and as centers of ecological activity, has only recently emerged as an area of academic interest as well as an issue related to the conservation and sustainable use of deep-sea fishes and related biological diversity, and demands further mapping, research and management plans (Freiwald and Roberts, 2005).

### 1.5. Vulnerability of deep-water corals

Increased interest in the economic exploitation of deep-water environments since the mid-1980s has raised concern about possible environmental impacts. Compared to other deep-sea ecosystems, these framework-forming cold-water corals are relatively well researched, but yield several characteristics that make them particularly vulnerable to a range of anthropogenic impacts. All deep-sea corals are extremely fragile due to their basic lifestyle, habit and slow growth rate; their inflexible structures are easily destroyed by almost any physical contact (Freiwald *et al.*, 2004). As surface attached animals, they cannot escape a heavy trawl or a current loaded with sediments or pollutants and as they grow in places that have rarely been subject to sudden environmental changes, they didn't develop responses to fast-occurring changes in their environment, which gives them a great disadvantage when facing disturbances (WWF, 2004). This has led to an increasing awareness that cold-water coral ecosystems deserve full protection both within countries' Exclusive Economic Zones and on the high seas (Davies *et al.*, 2011).

Many studies have recently raised the concern that coral reefs around the globe are threatened: impacts of anthropogenic activities are evident in almost every survey undertaken,

regardless of the depth at which the corals occur (Freiwald *et al.*, 2004). Assessments of these corals have shown that damage to their habitats may occur from human-induced threats such as commercial bottom trawling, oil and gas exploration and drill cuttings, dredging, sedimentation, waste disposal, dumping and pollution, bioprospecting and research activities, coral exploration and trade, and ocean acidification. Temperature extremes, excess nutrients, disease and strong currents, are also potential sources of historic mortalities (Gass and Roberts, 2006; Hain and Corcoran, 2004; Freiwald and Roberts, 2005; Turley *et al.*, 2007).

The development of more powerful and sophisticated technologies has enabled industry, including the fishing and oil and gas sectors, to access ocean depths previously out of reach, leading to the overexploitation and exhaustion of fish species that inhabit deep-water coral reefs. Recent scientific studies have shown that deep-water corals are being devastated by bottom trawling, the most severe threat to these communities, which results on fragmentation of coral reef habitat and increased mortality. Underwater observations of *Lophelia* sp. (200-400 m) reefs off Norway have confirmed that between 30-50% of the reefs have already been removed (Hain and Corcoran, 2004; Rogers, 2004; Witherell and Coon, 2001). In addition, there is warranted concern that seawater chemistry changes caused by the increase of anthropogenic carbon dioxide levels (ocean acidification) have the potential to alter the distribution and abundance of marine calcifying organisms that use calcium carbonate crystal structures (aragonite and calcite) to build their shells, liths and skeletons (corals, plankton such as coccolithophores and foraminiferans, shelled pteropods). As the pH and carbonate ions available in seawater decrease dramatically, it will be more difficult for marine calcifying organisms to form biogenic calcium carbonate (CaCO<sub>3</sub>) and corals are expected to build weaker skeletons that become more prone to breakage and/or experience slower growth rates (Davies *et al.*, 2008; Guinotte *et al.*, 2006; Maier, *et al.*, 2009).

Under these circumstances, the possible re-growth of damaged reefs and the restitution of their ecological function may take several hundreds or thousands of years and their removal or damage could have long-term effects on associated faunal communities (Fosså *et al.*, 2002; Roberts and Hirshfield, 2004; Roberts *et al.*, 2006; Rogers, 2004). Unfortunately, just as scientists have begun to understand the diversity, importance, vulnerability and role of deep-sea coral forests in the oceans, humans have developed technologies that profoundly disturb them, and so they became a topic of interest due to conservation concerns (Hain and Corcoran, 2004; Kellogg *et al.*, 2009; WWF, 2004).

In this context, some countries and regional bodies have recently enacted, or are in the process of establishing, regulations and management measures to protect a few reefs including protecting discrete areas from bottom disturbing activities, restricting gear size to limit the ability of fishermen to tow their gear through rough terrain where many deep-sea corals live, and prohibiting bottom trawling in areas that have been repeatedly fished by trawls in the past decade (Freiwald *et al.*, 2004; Witherell and Coon, 2001). However, vast deep-water resources are

primarily found in areas beyond national boundaries and jurisdiction, in the international waters of the High Seas, where the “freedom of the high seas” allows exploitation of natural resources (Rogers, 2004). One of the most urgent tasks today is therefore to develop a globally agreed procedure, covered by international law, to protect biodiversity in these vast global commons (WWF, 2004).

### **1.6. Study context and objectives**

It is evident that there are still large gaps in our knowledge about these ecosystems that need to be fulfilled. Scientists continue to discover, characterize, and research deep-sea coral ecosystems, and are trying to answer questions regarding their global distribution, abundance, biology, growth dynamics, carbonate production, geology, hydrography, microbiology and geochemistry, in order to fully understand the reef habitat, its structure and ecological function (Wienberg *et al.*, 2009). It is hoped that this knowledge will be used as a basis for further understanding of how the deep-sea species survive and disperse. Without this detailed information, it is going to be difficult to determine, and subsequently manage, potential anthropogenic impacts on these deep-water reef systems. These data are also directly applicable to the conservation of deep-sea ecosystems: detailed information of the location and status of coral communities will assist in the process of determining the best management approach to conserve what remains of these systems, and to promote recovery (Freiwald and Roberts, 2005). Finally, these fragile cold-water coral reefs have great ecological and socio-economic importance, and without urgent and precautionary action for their conservation, protection and sustainable management, the goods and services these magnificent reefs may supply could be lost forever (Freiwald *et al.*, 2004; Hain and Corcoran, 2004; WWF, 2004).

Recently, several fossil cold-water coral carbonate mounds, almost devoid of living corals, have been found along the Spanish and Moroccan margins in the Gulf of Cadiz (GoC) in a water depth between 400 and 960 m, suggesting that these margins once provided suitable conditions for their development. Cold-water corals grew associated to these carbonate mounds (and on top of escarpments in the close vicinity of mud volcanoes (Maignien *et al.*, 2011; Pirlet *et al.*, 2012; Wehrmann *et al.*, 2011; Wienberg *et al.*, 2009). Although cold-water corals are a common feature on the adjacent cliffs, mud volcanoes and open slope, reports on cold-water coral findings in this region are scarce, and refer mostly to dead coral framework and coral rubble, even though some living colonies have been reported (Morsoleto, 2009; Van Rooij *et al.*, 2011).

In this context, the development of a study project that focus the macrofaunal biodiversity of cold-water coral habitats and adjacent areas in the Gulf of Cadiz (NE Atlantic) is the focus of my research. The biological material used in this study was obtained during the cruises M2005 (64PE237), M2006 (64PE253) and M2007 (64PE268), onboard the R. V. *Pelagia* in 2005, 2006 and 2007, respectively, in several sites of the Moroccan margin of the El Arraiche province



(GoC). The objective of the present work is, therefore, to characterize the composition and structure of the benthic macroinvertebrate communities that live in association with different habitats of the Moroccan margin of the Gulf of Cadiz: carbonate mounds, cold-water coral reefs, the Pen Duick Escarpment; additionally, four mud volcanoes of the El Arraiche field that were sampled in the same cruises will also be examined.

The biological material collected during these cruises will therefore contribute to attain the following specific objectives:

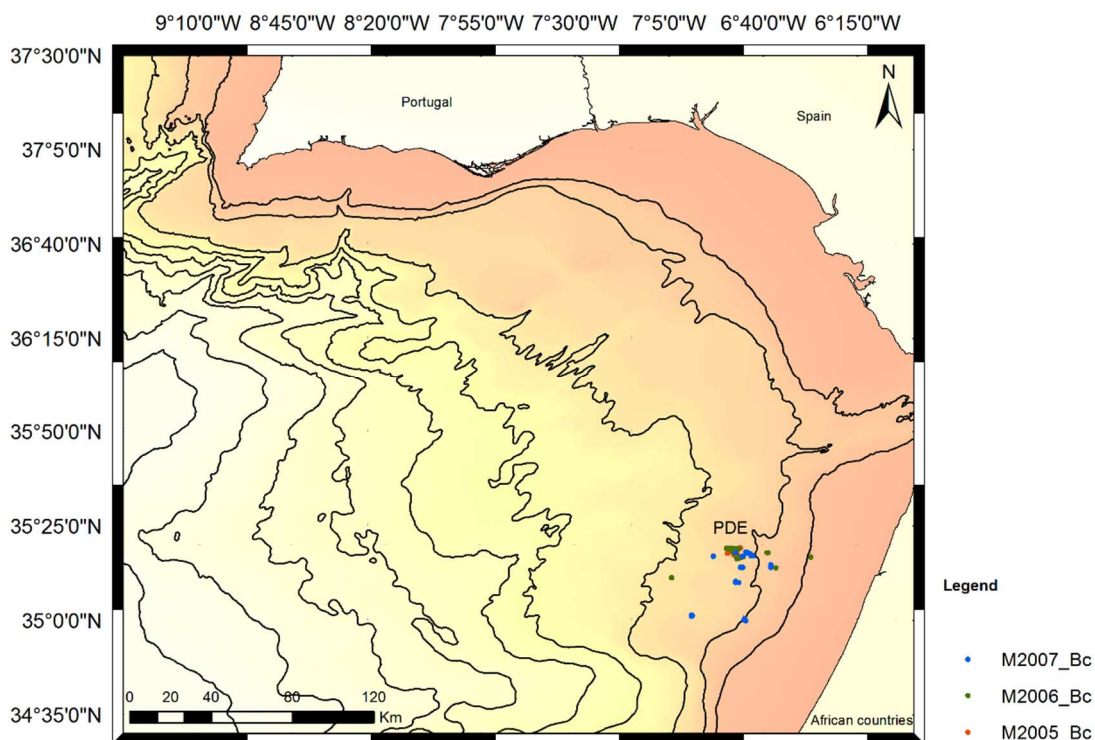
- i. to gain more information on the biodiversity and ecology of benthic macroinvertebrates;
- ii. to characterize and compare the diversity, abundance and the community structure of the macrofaunal assemblages from distinct features of the Gulf of Cadiz region;
- iii. to identify differences between mound and off mound areas, namely in terms of species richness, abundance and composition of the assemblages;
- iv. to determine the difference, in terms of biodiversity, between sites characterized by the presence of coral substrates with sites of soft sediment;
- v. to investigate possible differences in the macrofaunal communities according to a gradient of increasing depth.



## 2. METHODOLOGY

### 2.1. Study area

The Gulf of Cadiz (GoC) is a tectonically active area of the European continental margin that forms an E-W oriented re-entrant in the Northeast Atlantic margin, between 34°N to 37°15'N and 6°W to 9°45'W. It is enclosed by the Southern Iberian Peninsula and Northern Africa, west of the Strait of Gibraltar (**Figure 6**). The GoC is presently the most extensive cold seepage area known on the European margins and for more than a decade, the international marine scientific community has deployed considerable efforts in studying the occurrence of mud volcanism and adjacent habitats (Cunha *et al.*, 2013a; Vanreusel *et al.*, 2009). This area is characterized by a very complex geological history intimately related to plate tectonic interaction between Southern Eurasia and North Africa, and underwent several episodes of rifting, compressional deformation and strike-slip motion during its evolution, due to the northward movement of the African plate relative to Iberia (Pinheiro *et al.*, 2003; Van Rooij *et al.*, 2011).



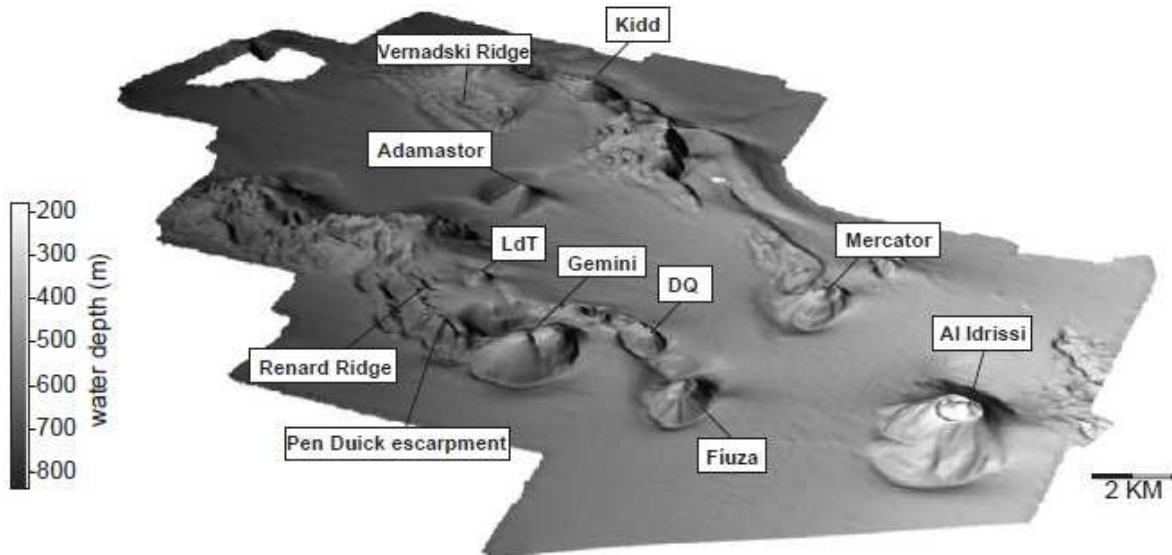
**Figure 6.** Bathymetric map of the Gulf of Cadiz area with the location of the boxcore (Bc) sampling sites in the Pen Duick Escarpment, mud volcanoes of the El Arraiche field and surrounding areas, during the cruises 64PE237, 64PE253 and 64PE268 (M2005, M2006 and M2007 respectively). Bathymetry from Zitellini *et al.* (2009).

In terms of oceanography, the Gulf of Cadiz is one of the most complex and interesting regions in the Atlantic Ocean. The geographic location and topography of this region locally determines the behavior of various major water masses; the present-day circulation patterns are thus characterized by strong oceanographic dynamics controlled by the exchange of NE Atlantic and Mediterranean water masses through the Strait of Gibraltar, giving rise to a particular hydrodynamic regime. This process creates two counter-flows on the GoC margin. The less saline, cooler water mass of the North Atlantic Central Water (<600 m depth) moves southeastwards into the Mediterranean, over the continental shelf, whilst the warmer, dense and more saline Mediterranean Outflow Water (MOW) flows from east to northwest over the continental slope (900 – 1,500 m depth). Once the MOW has left the basin, it moves north into the Atlantic Ocean. The interaction of different water masses with the seafloor at different depths is reflected in varying sea bottom current velocities and temperatures and is responsible for the distribution of highly variable seabed sediments along the margins of the GoC (De Haas *et al.*, 2005; Hernández-Molina *et al.*, 2006; Lobo *et al.*, 2000; Peliz *et al.*, 2007).

Cold-water coral reefs in the Gulf of Cadiz have been studied previously during various cruises (e.g. TTR cruises - UNESCO “*Training Through Research*” program, Moundforce cruise M2004). Although sometimes targeting mud volcanoes (MVs), during these cruises, geological, biological and geochemical studies were also carried out in order to understand the cold-water coral community structure and the formation of carbonate mounds. The El Arraiche area is part of a larger carbonate province in the southern part of the Gulf of Cadiz (**Figure 7**) and encompasses several mud volcanoes (e.g. Al Idrissi, Mercator; Lazarillo de Tormes, Gemini) and ridges (Vernadsky Ridge and Renard Ridge) (Rejas *et al.*, 2006; Van Rooij *et al.*, 2011). The mud volcanoes in this area are mildly active, as indicated by the occurrence of typical methane seep fauna, such as the siboglinid polychaetes (*Siboglinum* spp.) and chemosymbiotic bivalves (e.g. *Solemya elairrachensis*) (Pinheiro *et al.*, 2003; Rodrigues *et al.*, 2012; Van Rensbergen, *et al.*, 2005).

The Pen Duick Escarpment (PDE) is a prominent fault scarp at 525 m depth, with about 4.5 km length and 100 m height, located in the Renard Ridge, about 30 nautical miles off shore the Moroccan coast. A cluster of about 15 carbonate mounds, in a juvenile growth stage, unlike their giant counterparts in the Porcupine Seabight, has been recently discovered in the area, covering the PDE cliff top and base. These structures are distributed in water depths of 500-600 m, reaching up to 60 m in height and about 500 m in length at the base. They are formed predominantly by fossil scleractinean coral framework embedded in a silty to muddy sedimentary matrix (Van Rooij *et al.*, 2011; Wehrmann *et al.*, 2011). Video imagery seabed surveys and surface samples revealed the presence of reef-forming scleractinians (stony corals) such as *Lophelia pertusa*, *Madrepora oculata*, *Dendrophyllia alternata* and occasionally, *Dendrophyllia cornigera*, however, few or no living polyps of stony corals were observed (De Haas *et al.*, 2005; Pirlet *et al.*, 2012). Only Anthozoans such as *Chelidonisis aurantiaca*, colonies of the bamboo coral *Isidella elongata* and other octocorals were observed living among large patches of coral rubble, i.e. very

small branch fragments, sparsely distributed on the soft sediments. Nevertheless, the thick open framework of these coral graveyards hosts a thriving micro-habitat for several benthic species (Morsoleto, 2009; Van Rooij *et al.*, 2011).

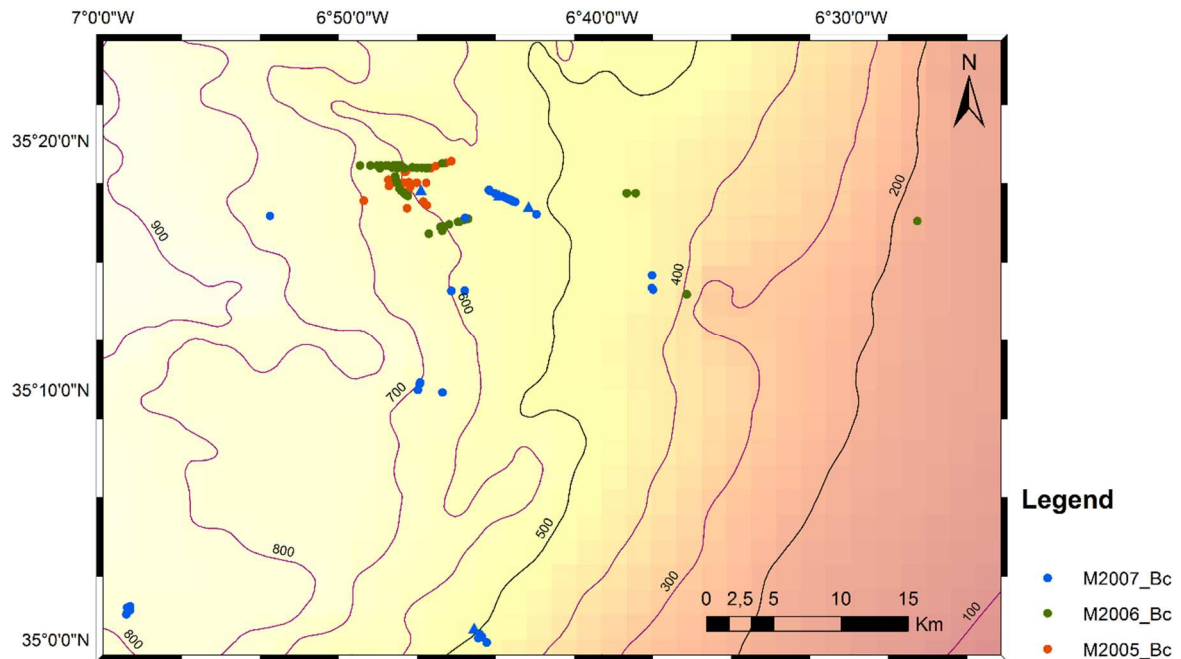


**Figure 7.** 3D morphology of the El Arraiche area at the Moroccan Atlantic margin derived from multibeam bathymetry. The Vernadsky and Renard Ridges form two visible topographic elevations. The locations of the most relevant sampling sites are signaled (e.g. Pen Duick Escarpment, Al Idrissi, Mercator, Gemini and Lazarillo de Tormes MVs (LdT). From Van Rensbergen *et al.* (2005).

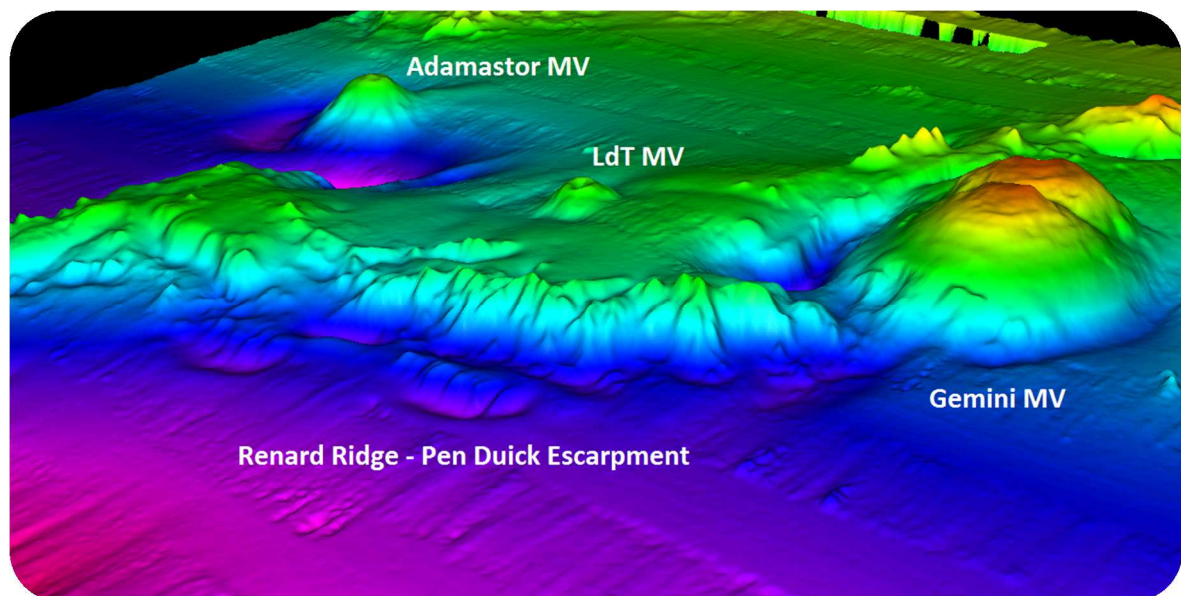
## 2.2. Sampling methodology

Sampling was undertaken in May-June 2005, October 2006 and May 2007 at the Moroccan margin, during the cruises M2005 (64PE237), M2006 (64PE253) and M2007 (64PE268), onboard the research vessel *Pelagia* (Royal Netherlands Institute for Sea Research, Royal NIOZ). The cruises were carried out within the framework of the European Science Foundation projects Moundforce (EUROMARGIN program, cruise 64PE237; De Haas *et al.*, 2005) and MiCROSYSTEMS (EuroDIVERSITY program, 64PE253 and 64PE268; De Haas *et al.*, 2006, 2007).

A total of 120 subsamples of box-corer (**Figure 8**) were collected during the three cruises, in water depths ranging from 220 to 900 m (see **ANNEXES I and II**), corresponding to distinct features of the El Arraiche area: the PDE (**Figure 9**), top of carbonate and coral mounds and off mound areas, and additionally also in Al Idrissi, Mercator, Gemini and Lazarillo de Tormes mud volcanoes. A few samples included in this study were also collected in sites of the Moroccan margin of outside of the El Arraiche boundaries.



**Figure 8.** Bathymetric map of the PDE and surrounding areas representing the sampled stations during the 64PE237, 64PE253 and 64PE268 cruises (M2005, M2006 and M2007, respectively). Bc: Boxcore sample. Bathymetry from Zitellini *et al.* (2009).



**Figure 9.** Bathymetric map of the Renard Ridge. The Pen Duick Escarpment and surrounding mud volcanoes (MV) are thereby represented: Adamastor, Lazarillo de Tormes (LdT) and Gemini. Modified from De Haas *et al.* (2006).

In this study, the material collected at the GoC consisted predominantly of silt and clay, typical deep-sea sediments. Coral debris were found in samples taken on the top of the escarpment as well as on the flanks of the mounds and at the lower plateau adjacent to the scarp. Most boxcore samples showed a soft layer of muddy clay at the top covering the coral debris. Other substrates could also be found, such as carbonate clasts and crusts, sandy admixture and/or foraminifera admixture as well as, echinoid spines, sponge spicules and bivalve and gastropod shells. The sediment colour ranged from yellowish brown to grayish olive or olive brown (De Haas *et al.*, 2005, 2006, 2007).

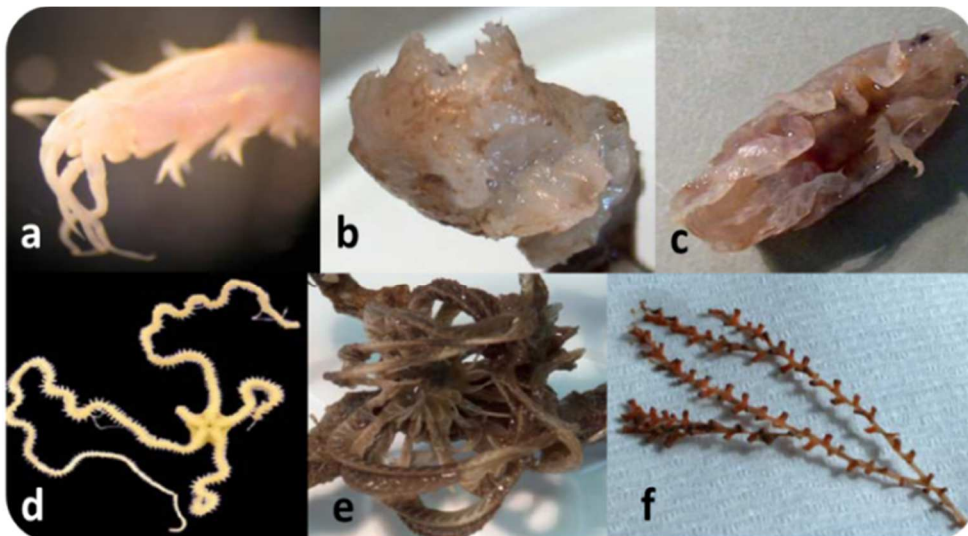
Sample processing (**Figure 10**) was initiated onboard immediately after recovery. The overlying water was siphoned through a 0.5 mm sieve in order to retrieve any small swimming fauna. During the 64PE237 cruise a variable volume of superficial sediment (approximately 25-30 cm) was collected and samples were considered qualitative. For the 64PE253 and 64PE268 cruises, whenever possible, one quarter of the box-corer ( $A= 4.9 \text{ dm}^2$ ) was processed. Whenever it was not possible to take such quantitative samples, non-quantitative samples were collected instead (in addition, any sediments remaining after subsampling for various purposes were also processed separately). All the sediment was carefully washed with seawater through 2 mm, 1 mm and 0.5 mm mesh-sieves, labeled and kept in 96% ethanol.

[Note that the author of this thesis did not participate in any of the three mentioned cruises. Onboard processing of the samples was carried out by Clara F. Rodrigues; sampling procedures were described according to De Haas *et al.* (2005, 2006, 2007). This study is the continuity of the works of Almeida (2009) and Casais (2012; unpublished results).]

At the Laboratory of Marine and Estuarine Ecology (Department of Biology, University of Aveiro), the samples were washed through a 500  $\mu\text{m}$  mesh sieve and the specimens were all sorted into major taxa under a stereoscopic microscope and kept again in 96% ethanol. Specimens were identified to the lowest practical taxonomic level, whenever possible to the species level. When the specimens were juveniles and/or were extremely damaged and if it was not possible to recognize whether they belong to the already identified taxa or to different ones, they were considered as “undetermined”. Specimens were deposited in the Biological Research Collection of the University of Aveiro (Department of Biology), where they remain available for further ecologic, taxonomic, morphologic, genetic or other necessary studies. Pictures of some of the specimens collected during the 64PE268 cruise are displayed at **Figure 11**.



**Figure 10.** Sampling processing onboard the R. V. *Pelagia* (cruise 64PE268). a) TV-guided box corer with mounted camera system; b) sediment washing for fauna sampling; c) subsampler of the box-core; d) fragment of coral retrieved by the box corer sampler. © Photos by Clara Rodrigues.



**Figure 11.** Examples of animals collected during the cruise 64PE268. a) Polychaeta (*Paradiopatra* cf. *hispanica*, Onuphidae); b) Porifera; c) Isopoda (*Natatolana* sp., Cirolanidae); d) Ophiuroidea; e) Crinoidea; f) Anthozoa (*Isidella elongata*). © Photos by Clara Rodrigues.



### 2.3. Data analysis

In order to maximize biodiversity data and because the sampling methodology of macrofauna involved both quantitative and non-quantitative procedures, the analyses were carried out using two approaches: a quantitative analysis (Q), with the quantitative biological data collected on the cruises 64PE253 and 64PE268 (known sampled area) and a qualitative analysis (QL), including the specimens collected during the cruise 64PE237 (unknown sampled area) and all the pooled data for each station sampled during the cruises 64PE253 and 64PE268. Organisms belonging to the taxonomic groups Nematoda, Copepoda, Ostracoda and Halacaridae were not included in the analysis since they are considered meiofaunal groups (Gerlach, 1971). All sessile, modular organisms such as sponges, cnidarians and bryozoans when included in the analyses, were coded 1 (presence) or 0 (absence). Samples with less than three taxa were discarded from the multivariate analysis. The biological data were used to estimate the taxa richness of each sample and in pooled groups of samples (e.g. according to type of geological feature, type of substrate or bathymetry). Density values were calculated for the quantitative data only, and expressed as individuals per ten square decimeters (ind.10dm<sup>-2</sup>).

All the statistical analyses were performed using the statistic package *PRIMER* V.6.1.13 (*Plymouth Routines In Multivariate Ecological Research*) (Clarke and Warwick, 2001). Multivariate analysis is used to assess for distributional patterns in the macrofaunal assemblages of the sampled sites. The abundance data was first organized into a sample vs species matrix, and *Non-metric Multi-Dimensional Scaling* (nMDS) was performed using the *Bray-Curtis* similarity measure, after square root transformation (Q analysis) or presence/absence transformation (QL analysis) of the data. The square root transformation has the effect of down-weighting the importance of the highly abundant species. The reduction of the data to presence/absence is necessary whenever qualitative analyses are performed. In the resulting MDS plot the placement of samples reflects the relative similarity of their biological communities (Clarke and Warwick, 2001).

In the context of this study, the null hypothesis (H<sub>0</sub>) states that there are no differences in the composition of macrofaunal assemblages in relation to the factors: “Geological Feature” (Test 1), “Presence of Hard Substrate” (coral or carbonate concretions; Test 2) and “Depth Zone” (Test 3). The R statistic obtained by this process is a useful comparative measure of the degree of separation of sites: large values (≈1) are indicative of complete separation of the groups, whereas small values (≈0) imply little or no segregation (Clarke and Warwick, 2001). An analysis of similarities by randomization/permutation tests (one-way ANOSIM: “*Analysis Of Similarities*”) was thus performed on the MDS results of samples according to the relevant factors (**Table I**). The allocation of each sample to a given category of these factors is shown in **ANNEX I**.

**Table I.** Criteria used for the multivariate analysis for qualitative (QL) and quantitative (Q) data. Samples not allocated to a given category in each factor were excluded (see also Annex I).

Test	Total number of samples: QL/Q	Group	Number of samples: QL/Q	Observations
<b>Geological Feature</b> (Test 1)	94/57	Pen Duick Escarpment (PDE)	41/25	Base, top and surrounding areas of PDE
		Mound (M) Off mound (OM)	26/11 14/11	Four mounds (64PE268) Flanks of MVs; stations in areas without evident mound structure
		Mud volcano (MV)	13/10	Crater, outer rim and upper flanks of MVs
<b>Presence of Hard Substrate</b> (Test 2)	73/44 (without MV samples)	Coral at surface (C)	41/25	Coral or carbonate concretions present
		Coral only below surface (CD)	17/12	Coral or carbonate concretions deeper in the sediment (downcore)
		Absence of coral (A)	14/7	Without coral, usually hemipelagic sediments
<b>Depth Zone</b> (Test 3)	81/47 (without MV samples)	Zone 1 (Z1)	38/16	< 560 m
		Zone 2 (Z2)	27/23	640 m < Z2 < 560 m
		Zone 3 (Z3)	16/8	> 640m

Density, taxa richness and other diversity indices were estimated for individual samples and for pooled groups of samples according to the three factors considered for ANOSIM tests. Taxa richness (S), Shannon-Wiener diversity index (H'), Pielou's evenness index (J'), Hurlbert expected taxa richness (ES<sub>(n)</sub>) and k-dominance curves (Hurlbert, 1971; Lamshead *et al.* 1983; Magurran, 2004) were calculated using the community analysis *PRIMER* v6 software (Clarke and Warwick, 2001). While all these indices were performed in the Q analysis, only S and ES<sub>(n)</sub> values were estimated in the QL analysis.

The biodiversity of the different groups was also assessed by constructing rarefaction curves. Rarefaction curves typically increase steeply at first, then gradually level off (indicating that additional sampling is yielding no additional relevant biodiversity information). The more diverse the community is the steeper and more elevated is the curve. Rarefaction curves allow making biodiversity comparisons amongst assemblages based of the maximum common number of individuals of the compared samples and also allow pooling of samples into groups (Clarke & Warwick, 2001; Gage & Tyler, 1991; Magurran, 2004).

For the analysis of  $\beta$ -diversity, a dissimilarity matrix based on the Bray-Curtis measure after square root transformation (Q analysis) and presence/absence transformation (QL analysis) were constructed.  $\beta$ -diversity is herein considered as the 'extent of species replacement or biotic change along environmental gradients'.  $\beta$ -diversity is of uttermost importance, since its values can be used to compare the habitat diversity of different study systems, according to Wilson and Shmida (1984). Diversity partitioning was subsequently assessed for species richness (S) and Shannon–Wiener index (H', only for the Q analysis). The total diversity ( $\gamma = \alpha + \beta$ ) is partitioned into the weighted average diversity within samples ( $\alpha$ ), according to the number of individuals pooled, and among samples ( $\beta$ ), and therefore the  $\beta$ -diversity can be estimated by  $\beta = \gamma - \alpha$ . To extend the partition across multiple scales ( $\beta$  1: within each group;  $\beta$  2: between distinct groups), the smallest sample unit for level 1 are individual box core samples, while for the upper levels sampling units are formed by pooling together the appropriate groups of nested samples. The total diversity can therefore be expressed as the percentage contributions of diversity in each hierarchical level. Partitioning was carried out by weighting each sample according to its respective abundance (see Cunha *et al.*, 2013a and references therein).

SIMPER analysis (Similarity Percentages - species contributions) was performed excluding modular organisms for the quantitative data (after square root transformation) and for qualitative data (after presence/absence transformation) to estimate the percentage contributions of each individual taxa to the average similarity within and average dissimilarity between groups of samples defined and tested *a priori* (Clarke & Warwick, 2001).

The taxa selected based on the SIMPER analyses were allocated to a trophic guild defined by the feeding mode, food type, size and source, and life style (trophic scheme adapted from MacDonald's *et al.*, 2010) according to the criteria shown on **Table II**.

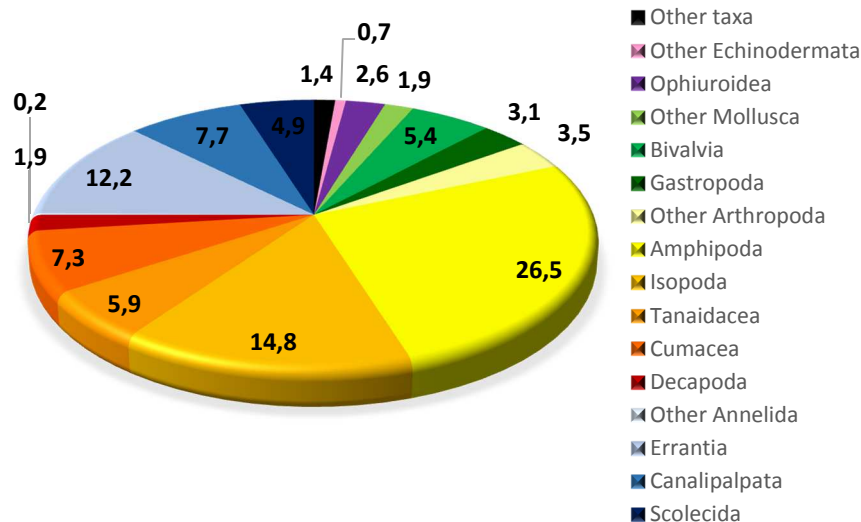
**Table II.** Parameters used to define the trophic guild and life style of the assemblages. Trophic scheme adapted from MacDonald's *et al.* (2010).

Parameter	Sub-parameter	Features
<b>Food type, size and source</b>	Food source	EP: epibenthic SR: surface; SS: subsurface
	Diet	Ca: carnivorous He: herbivorous Om: omnivorous
	Type/Size	sed: sediment pom: particulate organic matter mic: benthic microfauna mei: benthic meiofauna mac: benthic macrofauna
<b>Feeding mode</b>		<b>De:</b> deposit feeder, i.e. ingest sediments together with pom, mic <b>Dt:</b> detritus feeder, i.e. only ingests pom, mic <b>Su:</b> suspension feeder, i.e. feeds on pom, mic, zoo, from the water <b>Pr:</b> predator, i.e. eats live animals <b>Sc:</b> scavenger, i.e. carrion only <b>Ch:</b> chemosynthetic, i.e. with symbiotic bacteria <b>Gr:</b> grazer, i.e., feeds by scraping on algae or sessile animals <b>Br:</b> browser, i.e. feeds by tearing or gathering particular items
<b>Life style</b>	Motility	<b>M:</b> motile, i.e. capable of active movement <b>D:</b> discretely motile, i.e. able to move, but unnecessary for feeding <b>S:</b> completely sessile
	Habit	<b>F:</b> free living <b>T:</b> tubicolous <b>B:</b> burrow-dwelling, i.e. sedentary, living in burrows

### 3. RESULTS

A total of 5,227 specimens (modular organisms such as Bryozoa, Porifera and Cnidaria not accounted for) were examined during this study and ascribed to 426 taxa (458 when including modular organisms), from which 338 were identified to species level. Most taxa were identified to species level except for the phyla, Nemertea, Cephalorhyncha (Priapulida), Sipuncula, Echiura, and Brachiopoda. The complete list of identified taxa is given in **Annex III**.

Arthropoda were the richest group in terms of number of taxa (59.9% of the total number of taxa with 2,597 specimens, ascribed to 255 taxa), followed by Annelida (25.1%, 1,841 specimens, 107 taxa) and Mollusca (10.3%, 279 specimens, 44 taxa). Echinodermata are less well-represented (3.3%, 226 specimens, 14 taxa) whereas specimens from the “Other taxa” group account only with a total of 284 specimens in 6 taxa (**Figure 12**). Within the arthropods the order Amphipoda, was the richest subgroup in terms of taxa number (113), followed by Isopoda (63 taxa), while Polychaeta were mostly represented by the subclass Errantia (52 taxa) and the infraclass Canalipalpata (33 taxa). The classes Bivalvia (23 taxa) and Ophiuroidea (11 taxa) represent the richest groups of Mollusca and Echinodermata, respectively.



**Figure 12.** Percent contribution of the major faunal groups from all samples. Other taxa: Nemertea, Cephalorhyncha, Sipuncula, Echiura, Brachiopoda, Chordata; Other Echinodermata: Echinoidea, Holothuroidea, Crinoidea; Other Mollusca: Solenogastres, Caudofoveata, Scaphopoda; Other Arthropoda: Crustacea undetermined, Nebaliacea, Euphausiacea, Mysida, Sessilia, Scalpelliformes, Pycnogonida; Other Annelida: Oligochaeta.

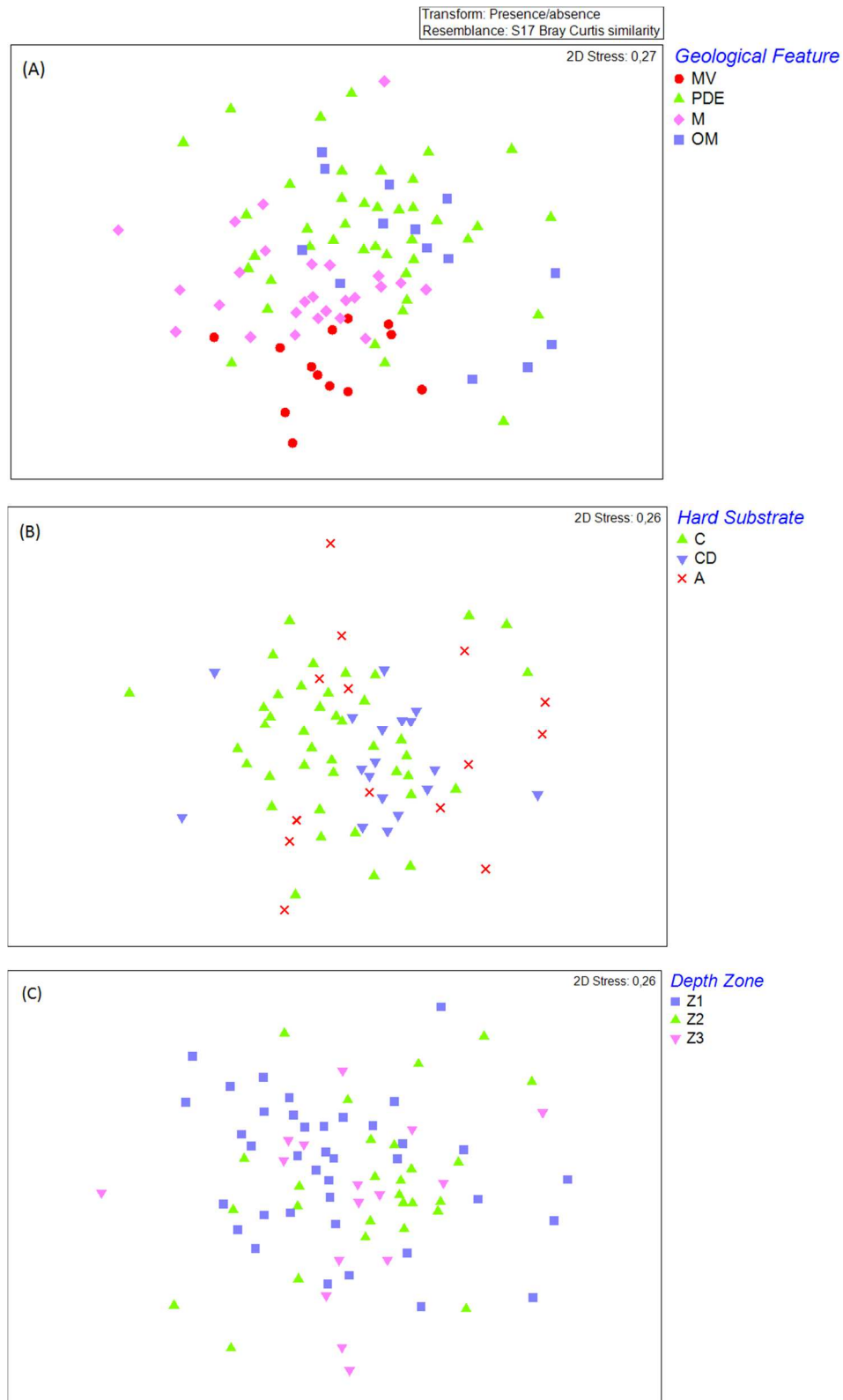
### 3.1. Multivariate analysis

**Effect of geological feature.** The MDS plot (**Figure 13A**) obtained for all the qualitative samples (QL) shows a large dispersion of samples from “Pen Duick Escarpment” (PDE) and “Off Mound” (OM) groups whereas samples from “Mud Volcanoes” (MV) and “Mound” (M) groups show a higher segregation. The same trend was observed in the quantitative (Q) analysis (not shown). Overall, differences between geological features are supported by the ANOSIM results both for QL and Q analyses (**Table III**, Test 1 A and B, respectively, Global R). Results are also coherent in both analyses for pairwise comparisons with significant differences between MV and OM, OM and M, and PDE and M and non-significant differences between PDE and OM (**Table III**, Test 1 A and B).

**Effect of hard substrate presence.** The MDS plot (**Figure 13B**) shows a high overlap of the different categories in this factor (QL analysis). Samples with coral at the surface (C) or coral at the sediment subsurface (CD) appear somehow closer while samples where coral is absent (A) are highly dispersed. The significance of the effect of substrate type is supported by the ANOSIM results in the QL analysis but not in the Q analysis (**Table III**, Test 2 A and B respectively, Global R; MDS for Q not shown). The subsequent pairwise comparisons (only QL analysis) show statistically significant differences between C and A, and CD and A, but not between C and CD (**Table III**, Test 2 A) suggesting a relevant effect of the presence of coral either at the surface or at the subsurface.

**Effect of depth.** The MDS plot from the QL analysis (**Figure 13C**) shows that samples from the three depth ranges were highly dispersed. Nevertheless, both QL and Q analyses showed significant statistically differences supported by the ANOSIM results (**Table III**, Test 3 A and B, Global R). In the QL analysis, pairwise comparisons showed significant differences between Z1 (top of the scarp) and Z2 (scarp itself), and between Z2 and Z3 (base of the escarpment), but non-significant differences between Z1 and Z3 (**Table III**, Test 3 A). Regarding Q analysis, only Z1 vs Z2 showed significant differences (**Table III**, Test 3 B).

Because the multivariate analyses support overall significant effects of the geological structure, presence of hard substrate and depth, further analyses and results will continue to be presented separately for the different factors and their respective categories.



**Figure 13.** MDS plots of the analyses performed on qualitative data (presence/absence) to assess the effect of: A) Geological Feature; B) Presence of Hard Substrate; C) Depth Zone. MV: Mud volcano; PDE: Pen Duick Escarpment; M: mound; OM: off mound; C: coral at surface; CD: coral at sediment subsurface; A: absence of coral; Z1: top of the scarp; Z2: scarp; Z3: base of the scarp.

**Table III.** Results of the ANOSIM one-way analysis for global and pairwise tests for the three analyzed factors: Geological Feature (Test 1), Presence of Hard Substrate (Test 2) and Depth Zone (Test 3). Analyses were performed using qualitative (A) and quantitative (B) data. n: number of samples analyzed. Number of used permutations in all tests: 999. \* significant; \*\* very significant; \*\*\* highly significant, ns: not significant.

	Sample statistic (R)	Significant Statistics	Significance level	n
<b>Geological Feature (Test 1 A)</b>				94
<b>Global test</b>	0.193	0	< 0.1% ***	
<b>Pairwise tests</b>				
MV vs M	0.194	15	1.6% *	
MV vs PDE	0.252	3	0.4% **	
MV vs OM	0.359	0	< 0.1% ***	
OM vs M	0.334	0	< 0.1% ***	
OM vs PDE	0.087	147	14.8% ns	
PDE vs M	0.169	0	< 0.1% ***	
<b>Presence of Hard Substrate (Test 2 A)</b>				73
<b>Global test</b>	0.100	35	3.6% **	
<b>Pairwise tests</b>				
C vs A	0.234	4	0.5% **	
C vs CD	-0.003	475	46.6% ns	
A vs CD	0.086	47	4.8% *	
<b>Depth Zone (Test 3 A)</b>				81
<b>Global test</b>	0.102	1	0.2% **	
<b>Pairwise tests</b>				
Z1 vs Z2	0.099	4	0.5% **	
Z2 vs Z3	0.120	27	2.8% *	
Z3 vs Z1	0.101	65	6.6% ns	
<b>Geological Feature (Test 1 B)</b>				57
<b>Global test</b>	0.254	0	< 0.1% ***	
<b>Pairwise tests</b>				
MV vs M	0.217	1	0.2% **	
MV vs PDE	0.401	0	< 0.1% ***	
MV vs OM	0.362	0	< 0.1% ***	
OM vs M	0.349	1	0.2% **	
OM vs PDE	0.038	274	27.5% ns	
PDE vs M	0.290	0	< 0.1% ***	
<b>Presence of Hard Substrate (Test 2 B)</b>				44
<b>Global test</b>	0.106	74	7.5% ns	
<b>Depth Zone (Test 3 B)</b>				47
<b>Global test</b>	0.100	22	2.3% *	
<b>Pairwise tests</b>				
Z1 vs Z2	0.135	2	0.3% **	
Z2 vs Z3	0.051	281	28.2% ns	
Z3 vs Z1	0.060	277	22.8% ns	



### 3.2. Species richness

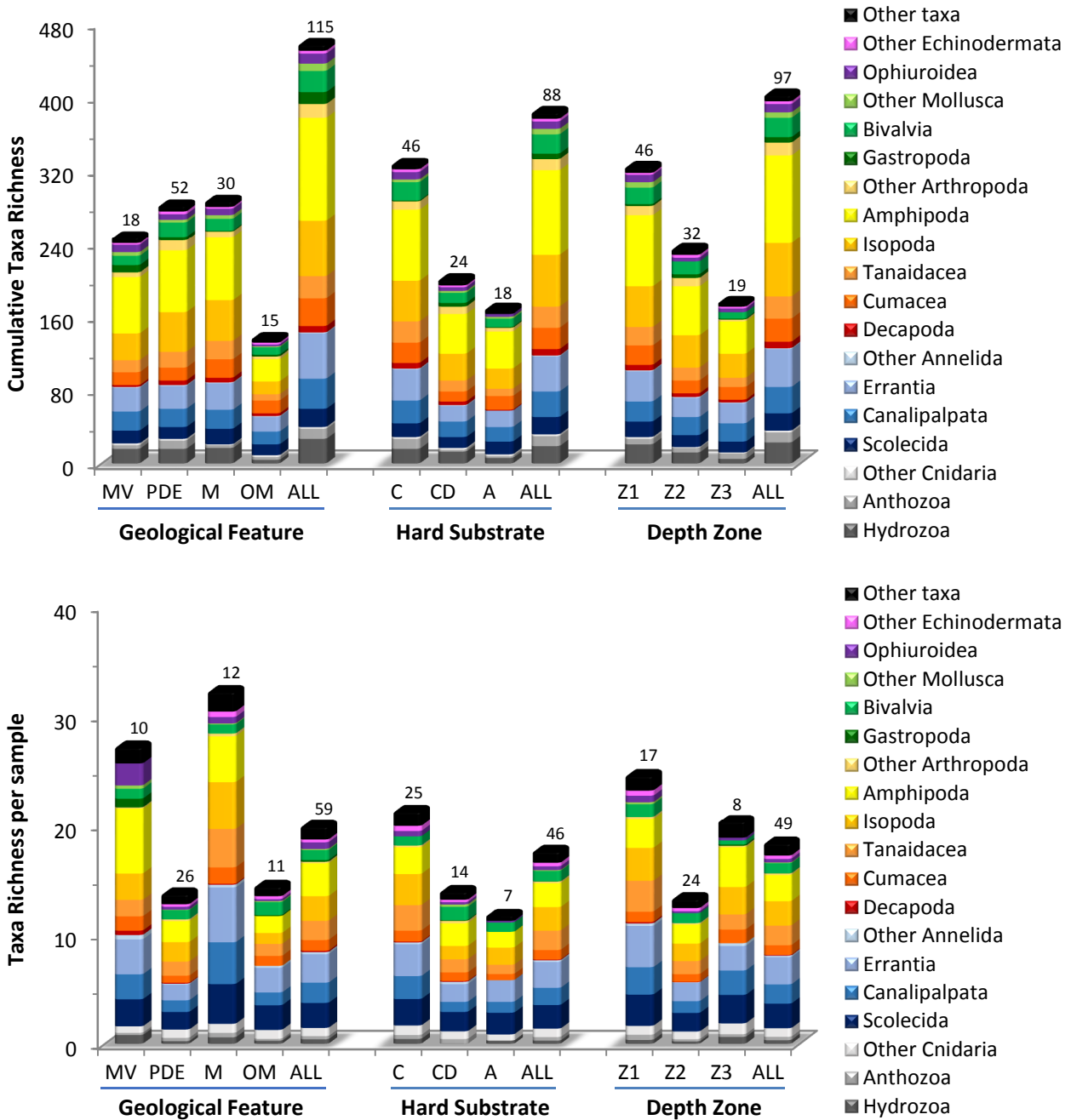
The cumulative taxa richness was estimated for the whole data set (**Figure 14 top**, QL analysis) whilst the average taxa richness per sample and percent contribution of the different taxonomic groups were estimated for the quantitative samples only (**Figure 14 bottom** and **Figure 15**, Q analysis).

**Geological feature.** From the total of 458 taxa (including modular organisms) recorded in this study 287 were found in the Pen Duick Escarpment (PDE, 52 stations), 282 in mound (M, 32 stations), 245 in mud volcanoes (MV, 18 stations) and 137 in off mound sites (OM, 15 stations). M stations yielded the highest cumulative number of Arthropoda (204 taxa, mainly Amphipoda, Isopoda and Tanaidacea) and Polychaeta (67 taxa). In contrast, the highest richness of Mollusca (23 taxa) was collected from the PDE stations. Mud volcanoes showed increased species richness of Ophiuroidea (8 taxa, mainly from Mercator and Al Idrissi MVs), Gastropoda (7 taxa from the Gemini MV) and Arthropoda (124 taxa); Gemini MV was the most taxa rich, with a total of 161 taxa (from 6 samples), followed by Lazarillo de Tormes MV (122 taxa in 8 samples) (data not shown). PDE and OM presented a similar average number of taxa per sample (14 and 15 taxa, respectively) despite the much lower sampling effort in OM. The taxa richness per sample observed in mounds and mud volcanoes was 2-fold higher (32 and 28 taxa, respectively). Again, there were important differences in the sampling effort which was much lower in MV than in M. Overall Arthropoda, and especially Amphipoda were the most speciose group but the relative contributions of the different taxonomic groups showed noticeable variations amongst the various geological features as shown in **Figure 15**: e.g. highest contribution of Amphipoda, Gastropoda and Ophiuroidea in MV, and of Polychaeta and Bivalvia in OM; lowest contribution of Bivalvia in M.

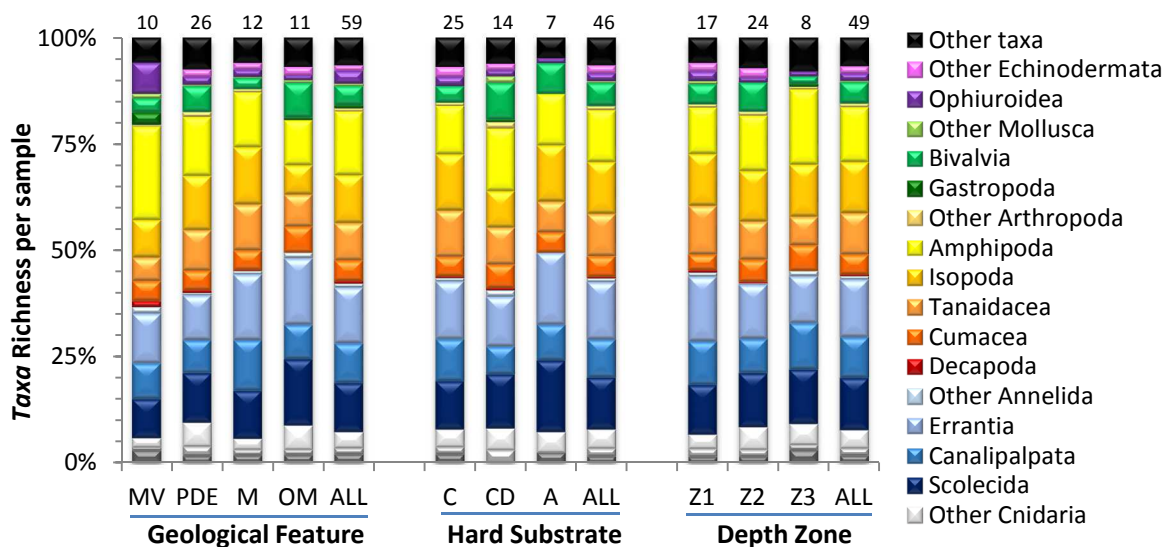
**Presence of hard substrate.** Samples characterized by the presence of hard substrates at the sediment surface (C) yielded the highest number of taxa (327) as well as the the highest average per sample (21). Taxa richness is comparatively decreased when coral is present only at the sediment subsurface (CD: 201 taxa in total; average of 14 taxa per sample) and even more when coral is absent (A: 169; 12). Once again, the difference in sampling effort (46 stations in C, 18 in A) must be taken in account (**Figure 14**). The Arthropoda and the Polychaeta, were represented by 173 and 74 taxa in C and only 86 and 48 in A and while Cnidaria were represented by 16 taxa in C and there were only 6 in A. The relative composition of the assemblages shows a higher contribution of Polychaeta in A and of Bivalvia in CD (**Figure 15**).

**Depth.** The observed cumulative number of taxa decreased from lower to higher water depths (324, 234 and 176 in Z1, Z2 and Z3, respectively). However, when comparing the average number of taxa per sample, Z1 and Z3 (25 and 21 taxa, respectively) are much richer than the scarp area (Z2: 13 taxa). Except for the low relative contribution of Mollusca and the absence of

Echinodermata in Z3 there are no noticeable differences in the assemblages from the different depth zones (Figure 15).



**Figure 14.** Cumulative taxa richness (top, QL analysis) and taxa richness per sample (bottom, Q analysis) in the different categories of the three analyzed factors. The total number of samples in each category is shown on top of the bars (mud volcano samples are included only in the factor “Geological Feature”; see **Annex I** for details). MV: mud volcano; PDE: Pen Duick Escarpment; M: mound; OM: off mound; C: coral at surface; CD: coral at subsurface; A: absence of coral; Z1, Z2 and Z3: top of scarp, scarp and base of scarp respectively; ALL: all samples.



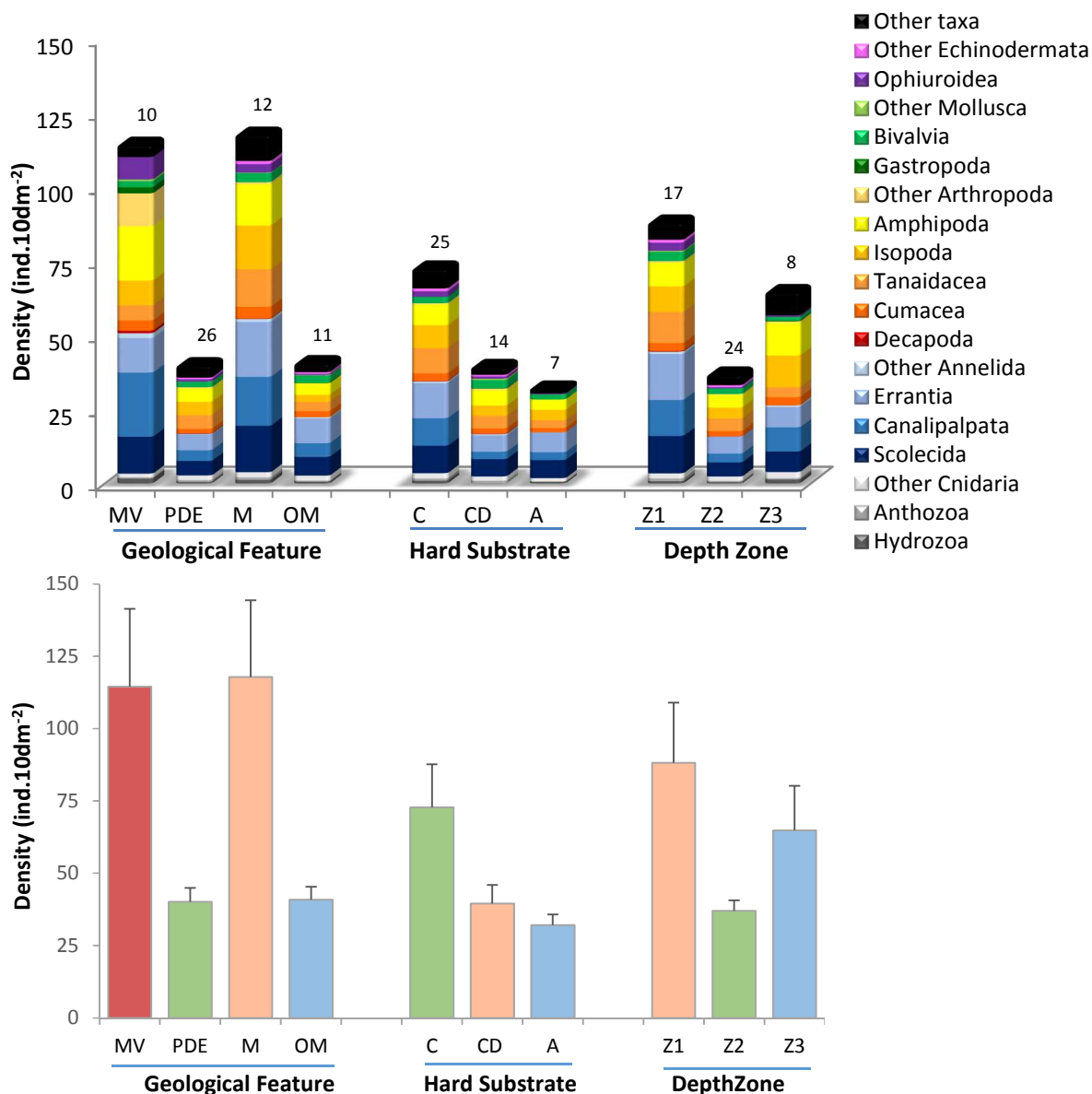
**Figure 15.** Percent contribution of the different taxonomic groups in each category of the three analyzed factors (Q analysis). The total number of samples pooled is shown on top of the bars. Abbreviations as in Figure 14.

### 3.3. Density

**Geological features.** The overall density (average number of individuals per 10 dm<sup>2</sup>) of the assemblages differed greatly amongst the different features (**Figure 16**). The highest number of individuals occurred in mounds (Average  $\pm$  SE: 117.9  $\pm$  26.5 ind. per 10dm<sup>2</sup>) and mud volcanoes (114.5  $\pm$  26.9 ind. per 10dm<sup>2</sup>), whilst the lowest occurred at the Pen Duick Escarpment and in off mound areas (40.1  $\pm$  4.8 and 40.8  $\pm$  4.5 ind. per 10dm<sup>2</sup>, respectively) (**Table IV**). Density differences among the four “Geological Features” were statistically assessed using the Student’s t-test: MV vs M and PDE vs OM comparisons were not significant ( $p > 0.05$ ). For MV vs PDE ( $t_s = 3.646$ ;  $df = 34$ ;  $p < 0.001^{***}$ ), MV vs OM ( $t_s = 2.861$ ;  $df = 19$ ;  $p < 0.01^{**}$ ), M vs PDE ( $t_s = 3.646$ ;  $df = 36$ ;  $p < 0.001^{***}$ ) and M vs OM ( $t_s = 2.831$ ;  $df = 21$ ;  $p < 0.01^{**}$ ) comparisons, differences were statistically significant. The benthic assemblages were characterized by different contributions of distinct taxa (**Figure 16 top**, and **Figure 17**). Polychaeta showed the highest density estimates in M (especially Scolecida and Errantia) and MV (mainly Canalipalpata), followed by Arthropoda, which are mainly represented by Amphipoda and Nebaliacea (included in “other Arthropoda”) in MVs and by the high densities of Amphipoda, Isopoda and Tanaidacea in M. MVs were also characterized by the highest densities of Ophiuroidea and Gastropoda and Mounds by high numbers of Sipuncula (“other taxa”). OM assemblages present a higher relative contribution of Polychaeta than Arthropoda, whilst PDE shows even abundances of both taxonomic groups.

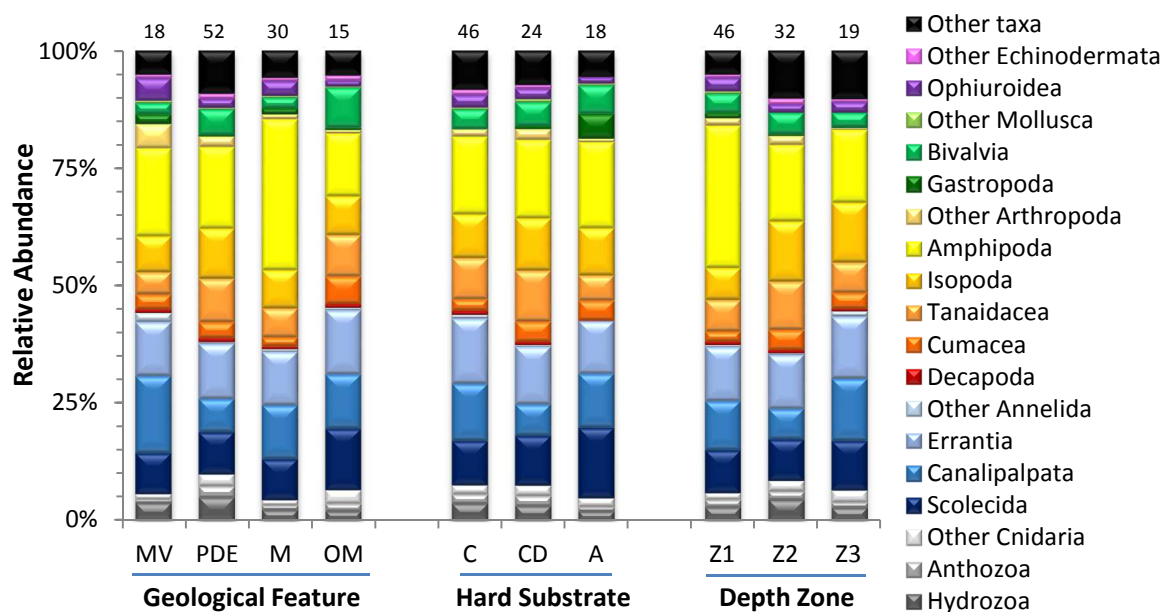
**Table IV.** Abundance and biodiversity data from the reduced matrix used for multivariate analysis (different numbers of taxa and/or samples were eliminated according the criteria explained in “Methodology”). n: number of samples; A: area sampled; N: number of individuals; D: density; SE: standard error; S: species richness; H': Shannon-Wiener diversity; J': Pielou's evenness; ES<sub>(50)</sub> and ES<sub>(100)</sub>: Hurlbert's expected number of species per 50 and 100 individuals, respectively; k<sub>1</sub>: abundance contribution of the first dominant species; MV: mud volcano; PDE: Pen Duick Escarpment; M: mound; OM: off mound; All: all samples; C: coral at surface; CD: coral at subsurface; A: absence of coral.

Sample	n	A (dm <sup>2</sup> )	N	D ± SE (ind.10dm <sup>-2</sup> )	S	H'	J'	ES <sub>(50)</sub>	ES <sub>(100)</sub>	k <sub>1</sub> (%)	First dominant species
<b>Quantitative analysis</b>											
<b>Geological Feature (GF)</b>											
MV	10	49.0	530	114.5 ± 26.9	131	4.08	0.838	31.9	52.0	15.6	<i>Siboglinum</i> spp.
PDE	26	127.4	469	40.1 ± 4.8	119	4.01	0.838	31.0	49.7	26.0	<i>Sipuncula</i> und.
M	12	58.8	683	117.9 ± 26.5	146	4.37	0.878	35.4	56.6	15.1	<i>Sipuncula</i> und.
OM	11	53.9	208	40.8 ± 4.5	72	3.79	0.885	30.9	48.2	28.8	<i>Paradiopatra</i> cf. <i>hispanica</i>
ALL	49	240.1	1360	59.3 ± 8.4	211	4.48	0.837	34.9	56.6		
<b>Hard Substrate (HS)</b>											
C	25	122.5	867	72.7 ± 14.9	172	4.36	0.847	34.1	55.1	27.6	<i>Sipuncula</i> und.
CD	14	68.6	248	39.5 ± 6.5	79	3.90	0.893	31.9	49.3	26.1	<i>P. cf. hispanica</i>
A	7	34.3	103	32.1 ± 3.7	51	3.62	0.919	32.0	50.1	25.5	<i>P. cf. hispanica</i>
Total (HS)	46	225.4	1218	56.4 ± 8.7	200	4.43	0.836	34.3	55.6		
<b>Depth Zone (DZ)</b>											
Z1	17	83.3	728	88.2 ± 20.8	150	4.30	0.858	34.0	54.3	14.0	<i>Sipuncula</i> und.
Z2	24	117.6	402	36.0 ± 3.7	116	4.05	0.853	32.0	51.7	29.3	<i>P. cf. hispanica</i>
Z3	8	39.2	230	64.8 ± 15.5	80	3.94	0.898	32.8	51.4	43.4	<i>Sipuncula</i> und.
Total (DZ)	59	289.1	1890	68.7 ± 8.6	253	4.58	0.828	35.4	57.9		
<b>Qualitative analysis</b>											
<b>Geological Feature (GF)</b>											
MV	13		1152		219			35.2	58.6		
PDE	41		1390		244			36.7	61.5		
M	26		2160		258			34.2	56.0		
OM	14		378		120			34.8	56.3		
ALL	94		5080		409			37.6	62.9		
<b>Hard Substrate (HS)</b>											
C	41		1919		295			38.1	64.0		
CD	18		690		166			35.3	57.7		
A	14		519		145			36.0	58.1		
Total (HS)	73		3128		337			37.9	63.4		
<b>Depth Zone (DZ)</b>											
Z1	38		2561		288			35.1	57.9		
Z2	27		866		195			35.5	59.1		
Z3	16		501		154			36.4	59.8		
Total (DZ)	81		3928		355			36.8	61.2		



**Figure 16.** Density of the macrofaunal assemblages in the different categories of the three analyzed factors. Contributions of the major faunal groups (top); Average and standard error (bottom). The total number of samples pooled is shown on top of the bars (top). Abbreviations as in Figure 14.

**Presence of hard substrate.** On average, C yielded greater average abundances ( $72.7 \pm 14.9$  ind. per  $10\text{dm}^2$ ) than CD ( $39.5 \pm 6.5$  ind. per  $10\text{dm}^2$ ) and A ( $32.1 \pm 3.7$  ind. per  $10\text{dm}^2$ ) (**Figure 16; Table IV**). However, statistical t-tests did not reveal significant differences between density averages of any pair of these groups ( $p > 0.05$ ), which may be explained by the high variability among replicates. Annelids were, in general, the most abundant taxa and dominant in all assemblages, and the assemblages do not seem to show clear differentiation patterns in terms of relative contributions of the different taxa to total abundance (**Figure 17**).



**Figure 17.** Relative abundance (%; Q analysis) of the major faunal groups in the different categories of the three analyzed factors. The total number of samples pooled is shown on top of the bars. Abbreviations as in Figure 14.

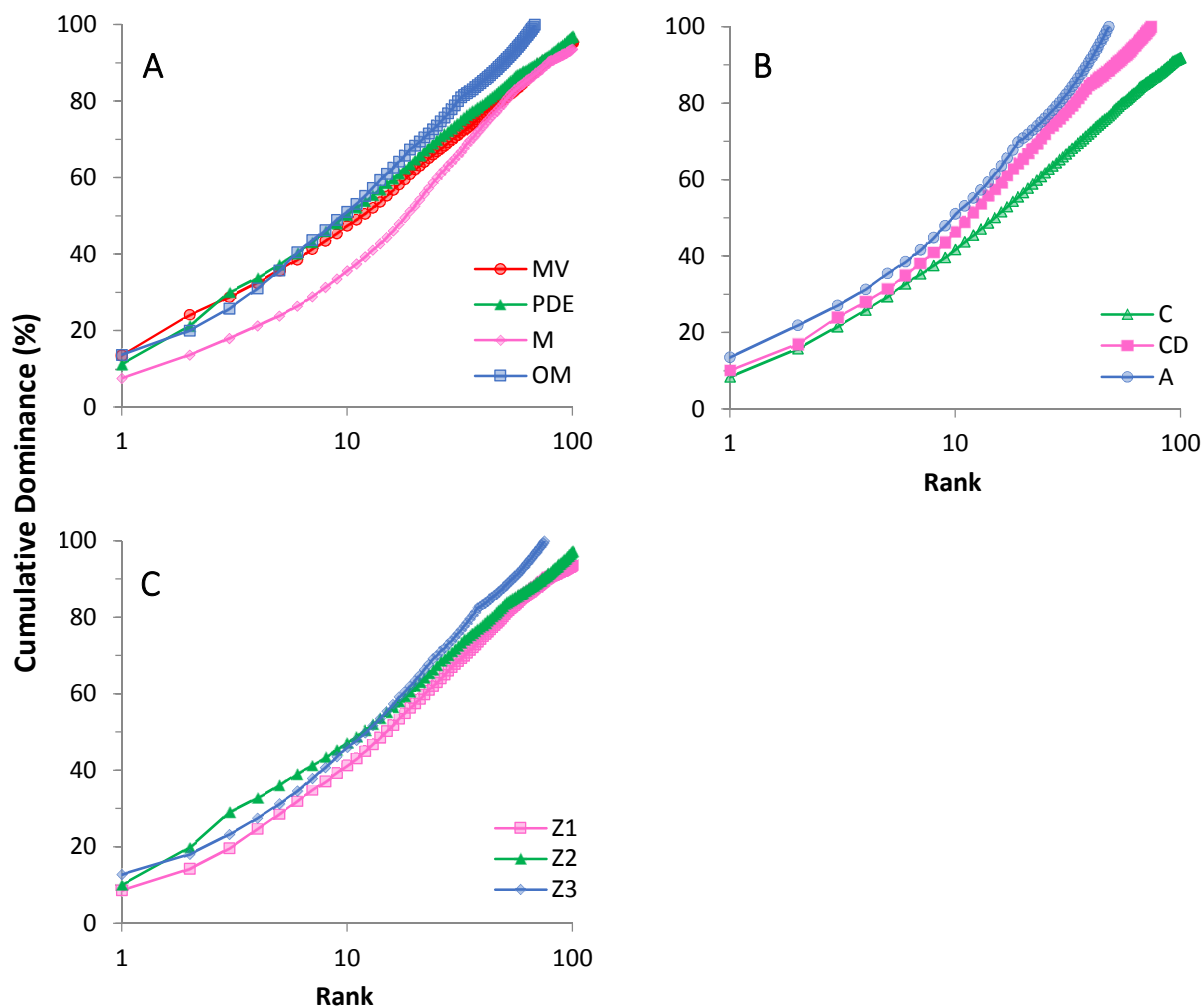
**Depth.** Macrofaunal densities (**Figure 16; Table IV**) were highest at shallower depths (Z1:  $88.2 \pm 20.8$  ind. per  $10\text{dm}^2$ ), decreasing greatly at the scarp ( $36.0 \pm 3.7$  ind. per  $10\text{dm}^2$ ), and finally increasing again at greater depths (Z3:  $64.8 \pm 15.5$  ind. per  $10\text{dm}^2$ ). Statistically significant differences were only found between Z1 and Z2 densities ( $t_s = 2.75$ ;  $df = 39$ ;  $p < 0.01^{**}$ ). In terms of relative abundance, Amphipoda are clearly dominant in Z1, but their numerical importance is reduced towards greater depths where Isopod and then Polychaeta increase their dominance (**Figure 17**). At Zone 1, Ophiuroids and Bivalves also reach their highest contributions for the total abundance of the benthic assemblage. The contribution of other taxa such as Sipuncula for Z1 and Z3 abundances is also noticeable.

### 3.4. Diversity indices

Overall and with very few exceptions, the studied assemblages show high diversity and low dominance (**Table IV, Figure 18**). The values of Shannon-Wiener diversity ranged from 3.62 to 4.37, evenness from 0.838 to 0.919, Hurlbert's number of expected taxa per 100 individuals varied from 48.2 to 56.6, and the contribution of the first dominant species from 15.1 to 43.4%.

**Geological features.** Mound assemblages show the highest diversity (M:  $H'$ : 4.37;  $ES_{(100)}$ : 56.6) followed closely by mud volcanoes whereas the off mound assemblages showed the lowest diversity values ( $H'$ : 3.79;  $ES_{(100)}$ : 48.2) but also the highest evenness ( $J'$ : 0.885) (**Table IV, Q analysis**). The k-dominance plots (**Figure 18A**) show overlapping curves of all assemblages except

for the M assemblage that is clearly below the three other. When the whole dataset is considered, the sampling effort is especially increased in PDE, and it is this area that yields the highest biodiversity ( $ES_{(100)}$ : 61.5; **Table IV**, QL analysis).



**Figure 18.** Comparison of k-dominance curves for macrofaunal assemblages (Q analysis) pooled by Geological Feature (A), Presence of Hard Substrate (B) and Depth Zone (C). Abbreviations as in Figure 14.

**Presence of hard substrate.** The assemblages from sites with coral framework at the sediment surface (C), presented the highest diversity values and lowest evenness ( $H'$ : 4.36;  $ES_{(100)}$ : 55.1;  $J'$ : 0.847) but the values in CD and A did not show a clear trend (**Table IV**, Q analysis). However, the k-dominance curves, all very close together but not overlapping, suggest that there is a gradient from the lowest dominance in C towards CD and A (**Figure 18B**). The QL analysis also further increased the difference in diversity between assemblages associated with C and the other two groups (**Table IV**, QL).

**Depth.** Although the shallow area yields higher diversity, the differences between depth zones are relatively small (**Table IV**, Q analysis) and when the whole dataset is used (QL analysis)

the results are not coherent as it is the deeper area yielding the highest diversity. The analysis of the k-dominance curves (**Figure 18C**) also shows overlapping curves confirming the lack of a clear trend in biodiversity in relation to the pre-defined depth zones.

### 3.5. Diversity partitioning

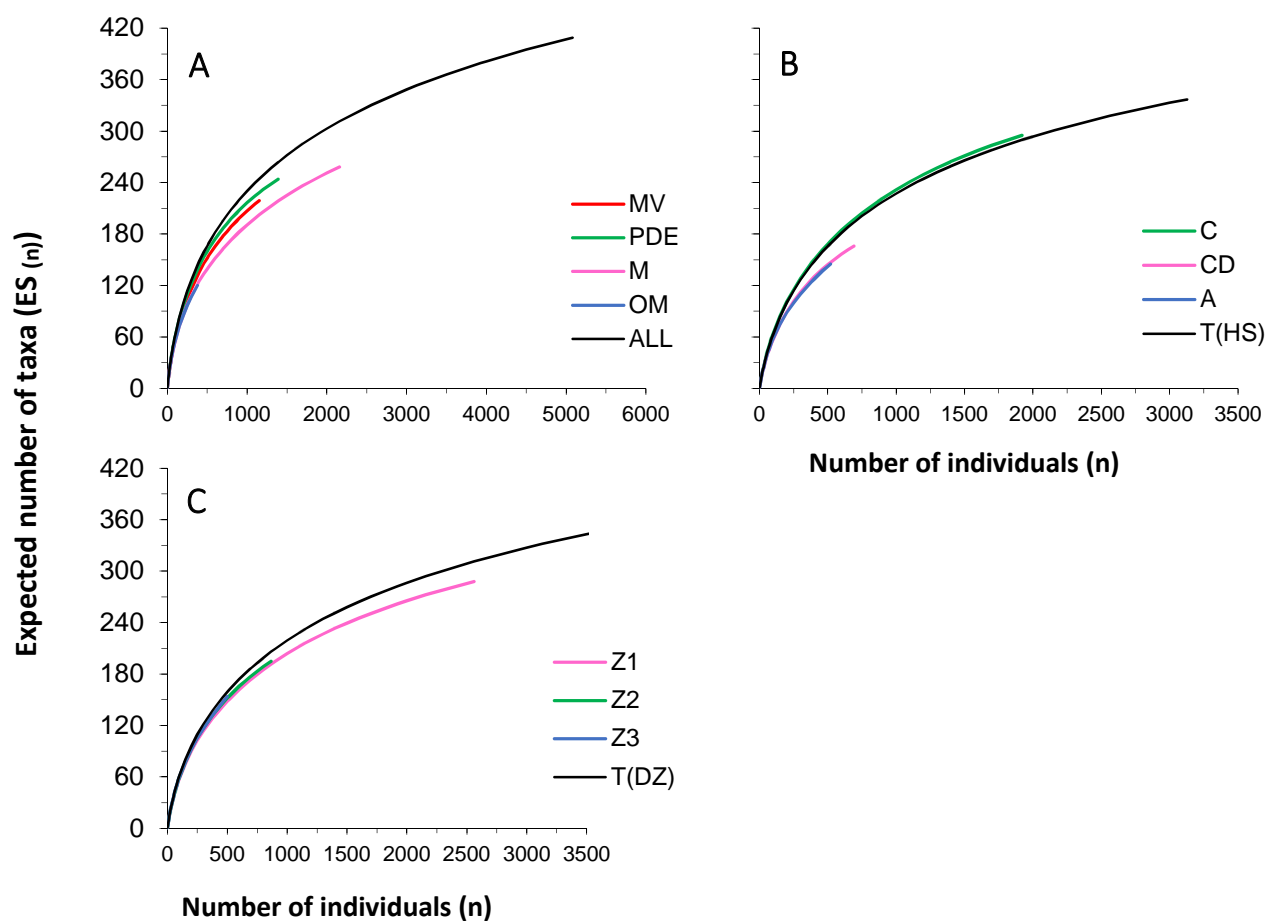
Patterns of  $\alpha$ -diversity and complementarity of the various categories within each analyzed factor are illustrated by the rarefaction curves (**Figure 19**). The steepness of the curves, both local (individual categories) and regional (pooled samples) indicates that the sampling effort was insufficient to assess the full biodiversity of the assemblages in the sampled area. These curves confirm the higher variability in  $\alpha$ -diversity of the assemblages from the different geological features with PDE emerging as the most biodiverse assemblage (**Figure 19A**). The three rarefaction curves representing assemblages from different substrate types (**Figure 19B**), are initially steep and overlapping; however, the C curve builds up into a more elevated position overlapping or even slightly above the curve of representing all samples (T). This indicates that C assemblages are locally highly diverse and have a much more important contribution to the regional diversity than the CD or A assemblages. In relation to depth, there is a high overlap of the curves representing assemblages from different zones (**Figure 19C**) which indicates that they are similar in terms of biodiversity. The more elevated curve of the whole assemblage (T – regional diversity) indicates that there is, however, some degree of complementarity among the depth sub-assemblages.

Diversity partitioning was assessed for species richness (S) and Shannon–Wiener index (H'), as shown in **Figure 20**. In terms on number of species (S), the contribution of the  $\alpha$ -diversity is globally rather low (9-15%); in the case of the assemblages pooled according to distinct Geological Features, for example (**Figure 20B**), the contribution of  $\alpha$ -diversity is 11.8% corresponding to an average number of species per sample of 18 for a grand total of 253. The partitioning of diversity in terms of species richness (S) is, therefore, mostly explained by  $\beta$ -diversity ( $\beta$ 1: within each group;  $\beta$ 2: between distinct groups): the contribution of  $\beta$ 1-diversity is lower for the factor geologic feature, increases for the factor depth and is higher for the factor substrate (increasing variability within categories) and the opposite trend is observed for  $\beta$ 2-diversity (decreasing variability between categories). This can be partly explained by the exclusion of the MV samples from the depth and substrate type analyses. According to these results, the assemblages of depth and substrate categories are not as distinctive as the ones from geological features.

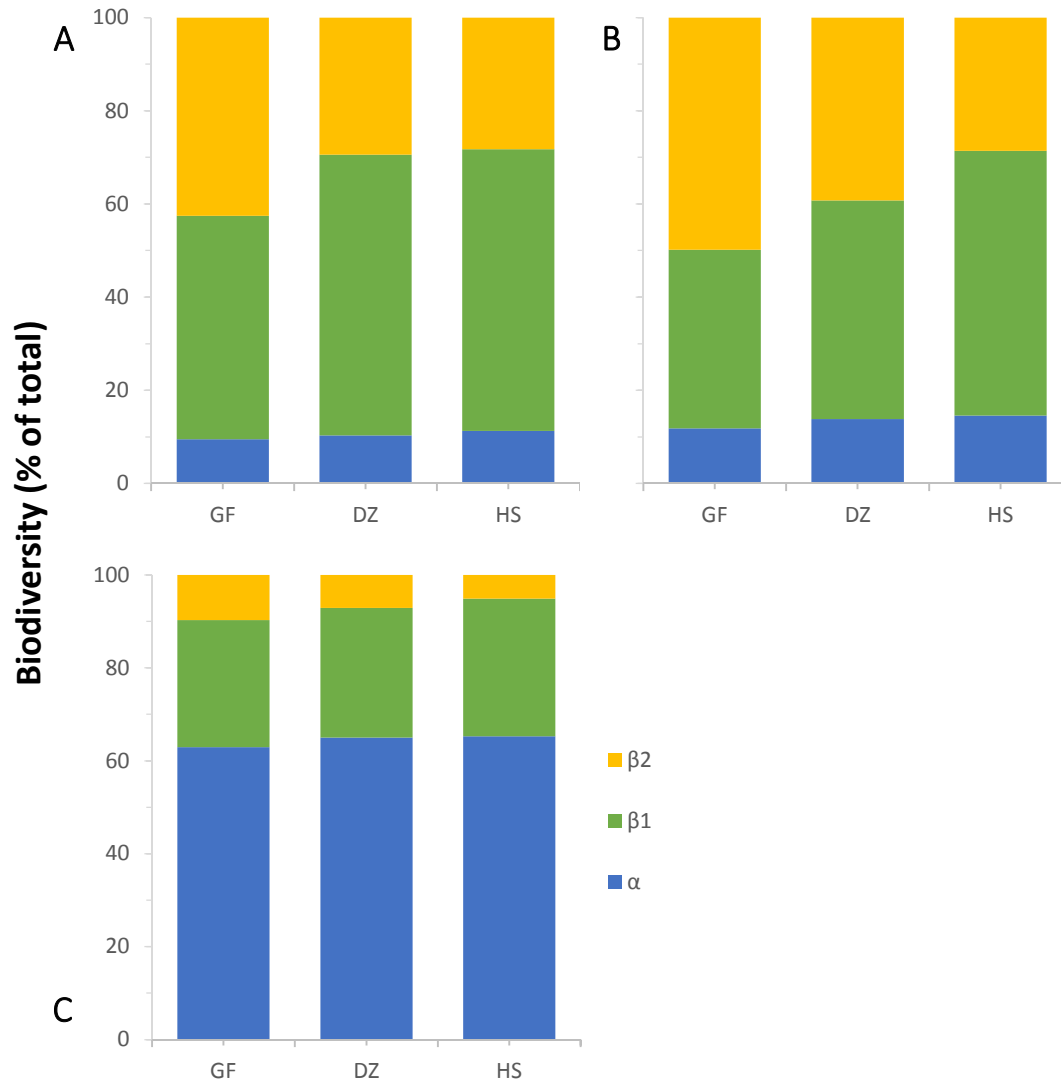
Partitioning of diversity is more similar between GF, DZ and HS samples according to the index related to the community structure (H'), on which the abundance is taken into account (**Figure 20C**). In this case,  $\alpha$ -diversity is the main contributor to the total diversity suggesting a structural integrity of the assemblages at small spatial scales (on average, about 62.9-65.2% of the total structural diversity is represented in each individual sample). This is higher than the proportion of the diversity explained by differences within and between groups ( $\beta$ 1: 27.3-28.6%,



$\beta_2$ : 5.1-9.7%). This pattern is thus linked to the consistency in the community structure, irrespective of the spatial grouping of the assemblages. Here, the dominance ranking (particularly because dominance is low in the majority of the samples) is more important in explaining the partition of diversity; in this case, the diversity between categories in each analyzed factor is only residual ( $\beta_2$ -small differences between groups of samples).



**Figure 19.** Rarefaction curves (Hulbert's expected number of taxa) for macrofaunal assemblages (QL analysis) pooled by Geological Feature (A), Presence of Hard Substrate (B) and Depth Zone (C). Abbreviations as in Figure 14. T(HS): pooled Hard Substrate samples; T(DZ): pooled Depth Zone samples.



**Figure 20.** Partition of taxonomic diversity for different indices. S: number of species (A and B, QL and Q analyses; respectively);  $H'$ : Shannon-Wiener diversity (C, Q analysis).  $\beta_1$ :  $\beta$ -diversity within groups of pooled samples;  $\beta_2$ :  $\beta$ -diversity between groups of pooled samples. GF: Geological Feature; DZ: Depth Zone; HS: Presence of Hard Substrate.

### 3.6. Species contributions

The most dominant and/or frequent species in the assemblages are generally retrieved by the SIMPER analysis as the major contributors for the similarity and dissimilarity of groups of samples (**Annex IV**). Overall, SIMPER results were determined by the high variability and heterogeneity in the composition of the assemblages: in the Q analysis, the average similarity (AS) within groups shows very low values (from 12.3% in A (type of substrate category) to a maximum of 24.2% in M (geological feature category)) and relatively high values of average dissimilarity (AD) for comparisons between groups (ranging from 80.5% (C/CD) to 88.2% (MV/OM)). This may be explained by the presence of a large number of species with low abundance and/or frequency, namely many singletons. Annelids were the main contributors (in terms of abundance and frequency of occurrence) to distinguish groups of samples. The polychaetes *Levinsenia* spp., *Paradoneis* spp., Maldanidae spp., *Siboglinum* spp., *Glycera lapidum* and *Paradiopatra* cf. *hispanica*, the tanaid *Atlantapseudes nigrichela*, the bivalve *Abra longicallus* and Sipuncula (undetermined species) were the main contributors on most analyses.

The most dominant/frequent taxa of the assemblages represented on SIMPER results were ascribed to a total of 14 different trophic guilds and six life style categories (**Annex IV**). Overall, surface deposit-feeders (SR-De) and subsurface deposit feeders (SS-De), were the most abundant and/or frequent, with 15 out of the 45 selected taxa (mainly Paraonidae, Maldanidae, Fauveliopsidae and Spionidae polychaetes, and by the Nuculidae and Semelidae bivalves; **Tables I-VI**). Higher trophic levels were also represented with 10 species of surface and subsurface predators on meio- and macrofauna (SR-Pr-mei, SS-Pr-mei, SR-Pr-mac, SS-Pr-mac) such as Phyllodocida polychaetes, and Oedicerotidae, Phoxocephalidae and Stenothoidae amphipods). Omnivorous categories (mostly SS-Om-mic) comprised only five taxa, three of which were asellote isopods). *Siboglinum* spp. were the only chemosymbiotic taxa (SR-Ch) and it was mostly recorded at MVs. Taxa were also grouped according their life style totaling six categories (M-F, M-B, D-B, D-F, D-T and S-T) (**Annex IV**). This analysis revealed that most of these species were motile, i.e. capable of active movement. Free living and tube-dwellers were less represented (eighth taxa, mostly polychaetes from which two are sessile: *Siboglinum* spp. and *Spiochaetopterus bergensis/typicus*). Burrow dwellers comprised Paranoid polychaetes and 3 species of the Phoxocephalid amphipod *Harpinia* sp.

**Geological features.** Differences between assemblages from distinct geological features are partly explained by taxa such as the siboglinids *Siboglinum* spp., which constitute major contributors for the distinction between mud volcanoes (where they attain their higher densities) and the other groups, characterized by much lower densities of these frenulate worms; the leptostracan *Nebalia* sp. and the amphipod *Stenothoe* cf. *marina/eduardi* also contribute for these differences, as they are absent (or present in much lower numbers) in the other assemblages (**Tables I and IV, Annex IV**). The dissimilarity between M, PDE and OM is explained mostly by

differences in abundance of Sipunculids, the polychaetes *Siboglinum* spp., Maldanidae spp., *Prionospio* spp. and *Spiochaetopterus bergensis/typicus* (higher abundance in M) the apseudomorph *A. nigrichela* (highest abundance in PDE), *P. cf. hispanica* and *G. lapidum* (higher abundance in OM).

**Presence of hard substrate.** Sipuncula, *A. nigrichela*, *Levinsenia* spp. (most abundant in A) and the bivalve *Ennucula corbuloides* represent some of the taxa that contributed for the dissimilarity between the C, CD and A assemblages (**Tables II and V, Annex IV**).

**Depth.** Some of the major contributors for the differences between Depth Zones are again: Sipuncula, *P. cf. hispanica*, *Levinsenia* spp., *A. nigrichela* and *S. bergensis/typicus* (**Tables III and VI, Annex IV**).

## 4. DISCUSSION

In the present study, 426 benthic invertebrate taxa were identified from 120 box-corer subsamples from water depths ranging between 220 and 900 m; the studied environments, at bathyal depths, along the Moroccan margins in the Gulf of Cadiz encompass elevated structures such as steep fault escarpments, carbonate mounds in association with fossil cold-water coral reefs and mud volcanoes. Unlike most of the sea floor, these distinctive habitats are known to host high abundances and diversity of deep-sea fauna (Jensen and Frederiksen, 1992; Raes and Vanreusel, 2006). These samples revealed that Arthropoda was the most speciose group (255 taxa), followed by Annelida (107 taxa), Mollusca (44 taxa), Cnidaria (40 taxa) and Echinodermata (14 taxa).

These outcomes are comparable to the ones obtained by several authors in other geographic areas. In 1992, the results from the first extensive quantitative sampling of deep-sea assemblages realized by Grassle and Maciolek indicated a much greater diversity of species than previously thought; these authors found that thousands of species of small invertebrates living on or in the sediments of the oceanic floor coexist in a shifting mosaic of microhabitats. In the same year, Jensen and Frederiksen (1992) identified a highly diverse, rich and facultative fauna associated to dead *Lophelia* colonies in the Faroe shelf off Scotland, comprising a total of 298 species, mainly dominated by Polychaeta (67 sp.), Bryozoa (45 sp.), Mollusca (31 sp.), Porifera (29 types), and Crustacea (15 sp.). Since then, increasing efforts to describe the biological diversity of cold-water coral reefs were recorded. In 2001, Koslow *et al.* sampled a group of 14 small seamounts south of Tasmania (Australia), from 660 to 1,700 m depth, obtaining 34 dredge samples (mouth area of 0.72 m<sup>2</sup>) with a dense, diverse (242 species) and highly endemic invertebrate benthic macrofauna, dominated by suspension feeders (30 species of corals), hydroids (14 sp.), sponges, bryozoans (14 sp.), crustaceans (69 sp.), echinoderms (58 sp.), annelids (29 sp.) and molluscs (10 sp.), which lived on the dead coral aggregates of *Solenosmilia variabilis*. Some years later, a study carried out in the southeastern U.S by Reed *et al.* (2006) documented 142 taxa of benthic invertebrates associated with six *L. pertusa* reefs, from which about 87% were sponges and cnidarians.

The present study demonstrated that when pooled according to mound (M) structures or by the presence of coral substrates (C), the macrofaunal assemblages were characterized by higher values of species richness, abundances, evenness, and low dominance, demonstrated by all Shannon-Wiener, Pielou's and  $ES_{(100)}$  indices. In the other hand, the macrofaunal assemblages of off mounds (OM) and areas of soft sediments without coral substrates (A) were represented by low values of species richness, abundance and taxa dominance and by high evenness. The distinction between M and OM features and C and A substrates was also supported by high statistical significant differences obtained from the ANOSIM tests and was clearly observed in the

rarefaction and k-dominance curves. However, a global high variability between individual samples was demonstrated by the high  $\alpha$ -diversity (according to H' measure) and scattering pattern on the MDS plots. This can be explained by the small sampled area of the replicates (only one quarter of the box-core) which may be insufficient to characterize the faunal communities. Nevertheless, the biogenic composition of the carbonate mounds and the physical presence of coral framework on the deep-sea sediments suggest an effect of enhancement of the communities richness and abundances on a regional scale.

The contrasting effect between coral mound structures and off mound sediment areas without coral framework was corroborated by other authors. Studies carried out on coral carbonate mounds from the Porcupine Seabight (Irish margin, NE Atlantic) revealed that these geological features are areas of high species diversity in the deep sea and therefore of particular ecological significance, as they provide a range of habitats associated with different substrate types that support the development of diverse and distinct faunal assemblages (Hall-Spencer *et al.*, 2009). In one of these studies, Henry and Roberts (2007) compared the macrobenthic biodiversity between on- and off-mound habitats, from a sampled area of 2.75m<sup>2</sup>, and found that mounds were three times more speciose (313 species), richer and with higher evenness and significantly greater Shannon's diversity than off-mounds (102 sp.). Overall, annelids (81 sp.), crustaceans (75 sp.), molluscs (47 sp.) and cnidarians (52 sp.) were the richest groups of these communities, as also verified in the present study.

Cold-water coral substrates are thus characterized by high habitat heterogeneity and can be further subdivided into smaller and different microhabitats. From these, dead coral fragments support the most diverse communities (macro- and megafauna), being the underlying sediment the least diverse (Jensen and Frederiksen, 1992). This can be attributed to the provision of elevated hard bottom substrates which are suitable surfaces for the settlement of a high abundance of filter/suspension feeders and sessile fauna (e.g. scleractinian corals, octocorals, sponges and other epifaunal organisms), sheltering function (low-disturbance environment) and higher habitat diversity of branched dead coral skeletons (framework) that enables the establishment of communities on and in between. The physical structure of the corals also provide habitat for a relatively unknown but biologically rich and diverse community of more mobile species such as fishes, crustaceans, mollusks, echinoderms, polychaete and sipunculan worms, among other macrofauna (Hall-Spencer *et al.*, 2009; Henry and Roberts, 2007; Reed *et al.*, 2006). Moreover, according to Freiwald and Roberts (2005), large biogenic structures as sediment-clogged coral framework are able to trap sedimented organic food; therefore they can be regarded as a possible hotspot of abundant food from seasonally deposited phytodetritus in a generally food-limited environment, which support enriched, diverse communities. Due to all these functions, cold-water coral reefs are considered biodiversity hotspots as they provide important niches for a highly diverse community of deep-water species (Roberts *et al.*, 2006).

Dead coral framework and associated substrates also constitute a highly diverse habitat for deep-sea meiofauna, namely nematods found in association with the sediment-clogged coral framework which are important food sources for abundant and diverse higher trophic levels of macro- and megafauna (Freiwald and Roberts, 2005; Raes and Vanreusel, 2005),

Four mud volcanoes of the El Arraiche province were also analysed in this study, as a distinct feature of the GoC seafloor. Macrofaunal assemblages from mud volcanoes were clearly differentiated from the other geological features analysed. The ANOSIM tests revealed highly significant differences further reflected by the closer arrangement of MV samples in the MDS plot and its segregation from the other groups of samples. Furthermore, MV assemblages were represented by high taxa richness (219 from the QL analysis) and densities, almost comparable to the mounds'. High values of  $H'$ ,  $J'$  and  $ES_{(100)}$  were also evident. The high density values found in these samples may be partly attributed to the relatively dominant chemosymbiotic *Siboglinum* spp., here represented by 100 individuals (14.08 ind.10dm<sup>-2</sup>). These samples also included a high number of other polychaete taxa (60) and arthropods, namely amphipods (61 in 124 taxa), and by high abundances of the leptostracan *Nebaliacea* sp. and ophiuroids of the family Amphiuridae. These results are thus comparable to the ones of Cunha *et al.* (2013a, b), that obtained 366 species from seven mud volcanoes at 350-4,000m depth, which is among the highest reported number of species for cold seeps. Annelida (136 sp., representing 52% of the total abundance) and Arthropoda (152 sp., 33%) were the most abundant and most species-rich phyla, while Mollusca and Echinodermata were less abundant and represented by a lower number of species (56 and 12 species, respectively) (Cunha *et al.*, 2013a).

Chemosynthetic-based communities, often dominated by frenulate siboglinids, have been found in several mud volcanoes in the Gulf of Cadiz. Therefore, the presence of *Siboglinum* spp. is indicative of the occurrence of reducing environments, as they are typically found in anoxic sediments in cold seeps, obtaining most of their nutrition from endosymbiotic sulphur-oxidising bacteria (Cunha *et al.*, 2011; Hilário and Cunha, 2008). In these mud volcanoes there is a high penetration of background fauna including a high number of peracarid crustaceans, polychaetes (namely the large-sized, mobile carnivores and omnivores Canalipalpata families Glyceridae, Polynoidae and Onuphidae), ophiuroids and buried bivalves of the families Solemyidae and Lucinidae. Solemyid bivalves such as *Solemya elarraichensis* (2 specimens were collected from the Gemini mud volcano, in the present study) also live in reducing sediments, with high organic-matter content, often at reduced oxygen concentrations; their nutrition is also via symbiotic chemoautotrophic bacteria (Rodrigues, 2009).

Depth-related changes in the abundance, biodiversity and composition of the assemblages present in the GoC are still poorly known. However, the analysis of the macrofaunal assemblages according to the depth gradient was rather inconclusive. The ANOSIM tests only revealed significant differences between Zones 1 and 2 (top of the scarp and the scarp itself),

which present contrasting values of taxa richness and abundances (higher at Z1). In the other hand, Zone 3 was characterized by intermediate abundances and the lowest taxa richness. Therefore, overall significant changes on the assemblages along a depth gradient were not verified; there was instead a notorious effect of the physical structure of the PDE in the composition of the benthic assemblages.

The results of the present study can also be compared with those of previous studies carried out in the GoC. Morsoleto (2009) identified a total of 145 macrobenthic invertebrates from nine quantitative box-corer samples (corresponding to a total area of 0.44m<sup>2</sup>) collected in the carbonate mound provinces along the Spanish and Moroccan margins of the GoC, between 520 and 907 m depth. Arthropoda, Annelida and Cnidaria were the major taxonomic groups represented on the samples. The author found highly heterogeneous assemblages with low dominance and high diversity, which is in accordance to the current results obtained from the Pen Duick Escarpment.

In terms of trophic guilds of the most abundant taxa there were increased contributions of deposit feeders feeding on small particles which form part of the sediment and benthic microfauna; most of them were represented by polychaetes but also by detritivorous crustaceans, several with a more opportunistic diet (e.g. caprellid amphipods such as *Liropus elongatus* and apseudomorph tanaisids). Apseudomorph tanaisids such as *Atlantapseudes nigrichela* use their appendages to collect detritus from the sediment but also may use a secondary filter feeding strategy. According to Cunha *et al.* (2013a), high-density assemblages in the deep-sea (e.g. mud volcanos) generally support higher trophic levels such as omnivores, carnivores or scavengers (e.g. Aciculata polychaetes), well represented by relatively common species such as *Glycera lapidum* and *Paradiopatra hispanica*, which were also well represented in the present study. In addition, sampling of the fauna from Porcupine Basin carbonate mounds also revealed that although most of the animals were suspension feeders there were also deposit feeding, carnivorous or omnivorous species (Hall-Spencer *et al.*, 2009).



#### 4.1. Final Remarks

Macrofaunal assemblage studies with relatively high taxonomic resolution like the present one are extremely important to the local knowledge on the faunal assemblages of the Gulf of Cadiz region but are also ultimately contributing to a comprehensive understanding of the composition and community structure of cold-water corals globally. The reduced bibliography for some groups hampered the identification of some species and highlighted the need to have more taxonomic review studies.

This study corroborates the hypothesis proposed by several authors, which claims that the presence of cold-water coral frameworks support a rich and highly diverse community of macrofaunal species found in several regions of the NE Atlantic (e.g. Gulf of Cadiz, Porcupine Seabight, Rockall Trough, Norwegian shelf). However, despite the increase of several studies in the Gulf of Cadiz in recent years, it is still difficult to estimate the overall biodiversity of this region. According to Cunha *et al.* (2013a), over 1000 taxa (unpublished data) were reported from the several locations and habitats of the GoC region (e.g. dead scleractinian cold water coral reefs, carbonate chimneys and concretions and several mud volcanoes), which exalts the importance of performing more researches in this highly rich area.

Nevertheless, the present-day destruction of scleractinian coral reefs by the increasing pressure of the industrial exploitation of the deep-sea may result in a great loss of habitat and biodiversity; the need of studying the biology, functioning and population dynamics of the benthic communities is a strong argument to improve our knowledge on the dramatic consequences of anthropogenic impacts on the deep-sea. In this context, scientific results are crucial for the development of conservation and management options in ecosystems which are affected by human activities. Future studies should thus focus these questions aiming to get more accurate estimates on the biodiversity of deep-sea coral areas.



## REFERENCES

- Almeida, M. D., 2009. Benthic Communities in Pen Duick Escarpment (Gulf of Cadiz). MSc thesis in Marine Biology. *Universidade de Aveiro*, 61 pp.
- Baillon, S.; Hamel, J.-F.; Wareham, V. E.; Mercier, A., 2012. Deep cold-water corals as nurseries for fish larvae. *Front Ecol Environ*, **10**: 351-356.
- Braga-Henriques, A.; Porteiro, F. M.; Ribeiro, P. A.; de Matos, V.; Sampaio, Í.; Ocaña, O.; Santos, R. S., 2013. Diversity, distribution and spatial structure of the cold-water coral fauna of the Azores (NE Atlantic). *Biogeosciences*, **10**: 4009-4036.
- Cairns, S. D., 2007. Deep-water corals: an overview with special reference to diversity and distribution of deep-water scleractinian corals. *Bulletin of Marine Science*, **81**: 311-322.
- Casais, J. F. M., 2012. Macrofauna associated with Cold-water Corals of Gulf of Cadiz – Results of the cruise MICROSYSTEMS 2007 (RV *Pelagia*). Research project for degree in Biology, Universidade de Aveiro.
- Clarke, K. R.; Warwick, R. M., 2001. Change in Marine Communities – An approach to Statistical Analysis and Interpretation, 2nd edition. *PRIMER-E*, Plymouth Marine Laboratory, UK.
- Cunha, M. R.; Paterson, G. L.; Amaro, T.; Blackbird, S.; de Stigther, H. C.; Ferreira, C.; Glover, A.; Hilário, A.; Kiriakoulakis, K.; Neal, L.; Ravara, A.; Rodrigues, C. F.; Tiago, A.; Billett, D. S., 2011. Biodiversity of macrofaunal assemblages from three Portuguese submarine canyons (NE Atlantic). *Deep-Sea Research II*, **58**: 2433-2447.
- Cunha, M.; Rodrigues, C.; Génio, L.; Hilário, A.; Ravara, A.; Pfannkuche, O., 2013a. Macrofaunal assemblages from mud volcanoes in the Gulf of Cadiz: abundance, biodiversity and diversity partitioning across spatial scales. *Biogeosciences*, **10**: 2553-2568.
- Cunha, M. R.; Matos, F. L.; Génio, L.; Hilário, A.; Moura C. J.; Ravara, A.; Rodrigues, C. F., 2013b. Are Organic Falls Bridging Reduced Environments in the Deep Sea? - Results from Colonization Experiments in the Gulf of Cádiz. *PLoS ONE*, **8**: 1-17.
- Davies, A. J.; Wisshak, M.; Orr, J. C.; Roberts, J. M., 2008. Predicting suitable habitat for the cold-water coral *Lophelia pertusa* (Scleractinia). *Deep-Sea Research I: Oceanographic Research Papers*, **55**: 1048-1062.
- Davies, A., J.; Guinotte, J. M., 2011. Global Habitat Suitability for Framework-Forming Cold-Water Corals. *PLoS ONE*, **6**: e18483.
- De Haas, H.; Mienis, F.; Shipboard Scientific Party, 2005. Cold water corals and carbonate mound formation at the Pen Duick Escarpment (Gulf of Cadiz) and Rockall Bank. Unpublished cruise report of R.V. *Pelagia* cruise M2005 (64PE237). *Royal Netherlands Institute for Sea Research*, Texel. 14 pp.
- De Haas, H., Shipboard Scientific Party, 2006. Seismic and sedimentological investigations of the carbonate mounds and mud volcanoes at the Pen Duick Escarpment and SE Gulf of Cadiz.

- Unpublished cruise report of R.V. Pelagia cruise M2006 (64PE253). *Royal Netherlands Institute for Sea Research*, Texel. 19 pp.
- De Haas, H., Shipboard Scientific Party, 2007. Seismic, sedimentological, geochemical and biological studies of carbonate mounds, mud volcanoes and mud diapirs in the SE Gulf of Cadiz. Unpublished cruise report of R.V. Pelagia cruise M2007 (64PE268). *Royal Netherlands Institute for Sea Research*, Texel. 26 pp.
- De Haas, H.; Mienis, F.; Frank, N.; Richter, T. O.; Steinacher, R.; de Stigter, H.; van der Land, C.; van Weering, T. C. E., 2009. Morphology and sedimentology of (clustered) cold-water coral mounds at the south Rockall Trough margins, NE Atlantic Ocean. *Facies*, **55**: 1-26.
- De Mol, B.; Van Rensbergen, P.; Pillen, S.; Van Herreweghe, K.; Van Rooij, D.; McDonnell, A.; Huvenne, V.; Ivanov, M.; Swennen, R.; Henriët, J. P., 2002. Large deep-water coral banks in the Porcupine Basin, southwest of Ireland. *Marine Geology*, **188**: 193-231.
- Fosså, J. H.; Mortensen, P. B.; Furevik, D. M., 2002. The deep-water coral *Lophelia pertusa* in Norwegian waters: distribution and fishery impacts. *Hydrobiologia*, **471**: 1-12.
- Frank, N.; Ricard E.; Lutringer-Paquet, A.; van der Land, C.; Colin, C.; Blamart, D.; Foubert, A.; Van Rooij, D.; Henriët J-P.; de Haas, H.; van Weering, T., 2009. The Holocene occurrence of cold water corals in the NE Atlantic: Implications for coral carbonate mound evolution. *Marine Geology*, **266**: 129-142.
- Freiwald, A.; Wilson, J. B., 1998. Taphonomy of modern deep, cold-temperate water coral reefs. *Historical Biology*, **13**: 37-52.
- Freiwald, A.; Fosså, J. H.; Grehan, A.; Koslow, T.; Roberts, J. M., 2004. Cold-water Coral Reefs. UNEP-WCMC Biodiversity Series, **22**: 1-85.
- Freiwald, A.; Roberts, J. M. (eds), 2005. Cold-Water Corals and Ecosystems. Springer, Heidelberg.
- Gage, J. D.; Tyler, P. A, 1991. Deep-sea biology: A natural history of organisms at the deep-sea floor. *Cambridge University Press*, Cambridge.
- Gass, S. E.; Roberts, J. M., 2006. The occurrence of the cold-water coral *Lophelia pertusa* (Scleractinia) on oil and gas platforms in the North Sea: Colony growth, recruitment and environmental controls on distribution. *Marine Pollution Bulletin*, **52**: 549-559.
- Gerlach, S. A., 1971. On the Importance of Marine Meiofauna for Benthos Communities. *Oecologia* (Berl.), **6**: 176-190.
- Grassle, F.; Maciolek, N., 1992. Deep-sea species richness: regional and local diversity estimates from quantitative bottom samples. *The American Naturalist*, **139**: 313-341.
- Guinotte, J. M.; Orr, J.; Cairns, S.; Freiwald, A.; Morgan, L.; George, R., 2006. Will human-induced changes in seawater chemistry alter the distribution of deep-sea scleractinian corals? *Front Ecol Environ*, **4**: 141-146.
- Hain, S.; Corcoran, E., 2004. The status of the cold-water coral reefs of the world. In: Wilkinson, C. (ed). *Status of Coral Reefs of the World: 2004*. 1: 115-135.

- Hall-Spencer, J.; Allain, V.; Fosså, J. H., 2002. Trawling damage to Northeast Atlantic ancient coral reefs. *Proceedings of the Royal Society of London, B*, **269**: 507-511.
- Hall-Spencer, J. M., Stehfest, K. M., Wheeler, A. J., 2009. Assessment of Coral Carbonate Mounds in the OSPAR area and the development of a monitoring program. OSPAR Commission, 26 pp.
- Hernández-Molina, F. J.; Llave, E.; Stow, D. A. V.; García, M.; Somoza, L.; Vázquez, J. T.; Lobo, F. J.; Maestro, A.; Díaz del Río, V.; León, R.; Medialdea, T.; Gardner, J., 2006. The contourite depositional system of the Gulf of Cádiz: A sedimentary model related to the bottom current activity of the Mediterranean outflow water and its interaction with the continental margin. *Deep-Sea Research II*, **53**: 1420-1463.
- Hilário, A.; Cunha, M. R., 2008. On some frenulate species (Annelida: Polychaeta: Siboglinidae) from mud volcanoes in the Gulf of Cadiz (NE Atlantic). *Scientia Marina*, **72**: 361-371.
- Hansson, L.; Agis, M.; Maier, C.; Weinbauer, M. G., 2009. Community composition of bacteria associated with cold-water coral *Madrepora oculata*: within and between colony variability. *Marine Ecology Progress Series*, **397**: 89-102.
- Henry, L.-A.; Roberts, J. M., 2007. Biodiversity and ecological composition of macrobenthos on cold-water coral mounds and adjacent off-mound habitat in the bathyal Porcupine Seabight, NE Atlantic. *Deep-Sea Research I*, **54**: 654-672.
- Hermione, 2012. *Hotspot Ecosystem Research and Man's Impact On European Seas*. Available at <http://www.eu-hermione.net/> (last visited in January, 2012).
- Hurlbert, S., 1971. The Nonconcept of Species Diversity: A Critique and Alternative Parameters. *Ecology*, **52**: 577-586.
- Jensen, A.; Frederiksen, R., 1992. The fauna associated with the bank-forming deepwater *Lophelia pertusa* (Scleractinia) on the Faroe shelf. *Sarsia*, **77**: 53-69.
- Kellogg, C. A.; Lisle, J. T.; Galkiewicz, J. P., 2009. Culture-Independent Characterization of Bacterial Communities Associated with the Cold-Water Coral *Lophelia pertusa* in the Northeastern Gulf of Mexico. *Applied and Environmental Microbiology*, **75**: 2294-2303.
- Koslow, J. A.; Gowlett-Holmes, K.; Lowry, J. K.; O'Hara, T.; Poore, G. C. B.; Williams, A., 2001. Seamount benthic macrofauna off southern Tasmania: community structure and impacts of trawling. *Mar Ecol Prog Ser*, **213**: 111-125.
- Lamshead, P.; Platt, H.; Shaw, K., 1983. The detection of differences among assemblages of marine benthic species based on an assessment of dominance and diversity. *Journal of Natural History*, **17**: 859-874.
- Lebar, M. D.; Heimbegner, J. L.; Baker, B. J., 2007. Cold-water marine natural products. *Natural Product Reports*, **24**: 774-797.
- Lobo, F. J.; Hernández-Molina, F. J.; Somoza, L.; Rodero, J.; Maldonado, A.; Barnolas, A., 2000. Patterns of bottom current flow deduced from dune asymmetries over the Gulf of Cadiz shelf (southwest Spain). *Marine Geology*, **164**: 91-117.
- Lophelia*, 2012. Available at <http://www.lophelia.org/> (last visited in November, 2011).

- Maier, C.; Hegeman, J.; Weinbauer, M. G.; Gattuso, J.-P., 2009. Calcification of the cold-water coral *Lophelia pertusa* under ambient and reduced pH. *Biogeosciences*, **6**: 1671-1680.
- Maignien, L.; Depreiter, D.; Foubert, A.; Reveillaud, J.; de Mol, L.; Boeckx, P.; Blamart, D.; Henriët, J.-P.; Boon, N., 2011. Anaerobic oxidation of methane in a cold-water coral carbonate mound from the Gulf of Cadiz. *Int J Earth Sci*, **100**: 1413-1422.
- Macdonald, T. A.; Burd, B. J.; Macdonald, V. I.; van Roodselaar, A., 2010. Taxonomic and feeding guild classification for the marine benthic macroinvertebrates of the Strait of Georgia, British Columbia. *Can. Tech. Rep. Fish. Aquat. Sci.*, **2874**: 64 pp.
- Magurran, A. E., 2004. Measuring Biological Diversity. *Blackwell*, Oxford, United Kingdom. 215 p.
- Masson, D. G.; Bett, B. J.; Billett, D. S. M.; Jacobs, C. L.; Wheeler, A. J.; Wynn, R. B., 2003. The origin of deep-water, coral-topped mounds in the northern Rockall Trough, Northeast Atlantic. *Marine Geology*, **194**: 159-180.
- Mienis, F.; de Stigter, H. C.; White, M.; Duineveld, G.; de Haas, H.; van Weering, T. C. E., 2007. Hydrodynamic controls on cold-water coral growth and carbonate-mound development at the SW and SE Rockall Trough Margin, NE Atlantic Ocean. *Deep-Sea Research I: Oceanographic Research Papers*, **54**: 1655-1674.
- Mienis, F.; van der Land, C.; de Stigter, H. C.; van de Vorstenbosch, M.; de Haas, H.; Richter, T.; van Weering, T. C. E., 2009. Sediment accumulation on a cold-water carbonate mound at the Southwest Rockall Trough margin. *Marine Geology*, **265**: 40-50.
- Morsoleto, F. M. S., 2009. Biodiversity of Cold-water Coral Reefs in the Gulf of Cadiz (NE Atlantic). *MSc thesis in Marine Biology*. Universidade de Aveiro, 40 pp.
- Mortensen, P. B.; Hovland, M. T.; Fosså, J. H.; Furevik, D. M., 2001. Distribution, abundance and size of *Lophelia pertusa* coral reefs in mid-Norway in relation to seabed characteristics. *J. Mar. Biol. Ass. U.K.*, **81**: 581-597.
- Naumann, M. S.; Orejas, C.; Wild, C.; Ferrier-Pagès, C., 2011. First evidence for zooplankton feeding sustaining key physiological processes in a scleractinian cold-water coral. *The Journal of Experimental Biology*, **214**: 3570-3576.
- Peliz, A.; Dubert, J.; Marchesiello, P.; Teles-Machado, A., 2007. Surface circulation in the Gulf of Cadiz: Model and mean flow structure. *J. Geophys. Res.*, **112**: 1-20.
- Pinheiro, L. M.; Ivanov, M. K.; Sautkin, A.; Akhmanov, G.; Magalhães, V. H.; Volkonskaya, A.; Monteiro, J. H.; Somoza, L.; Gardner, J.; Hamouni, N.; Cunha, M. R., 2003. Mud volcanism in the Gulf of Cadiz: results from the TTR-10 cruise. *Marine Geology*, **195**: 131-151.
- Pirlet, H.; Wehrmann, L. M.; Brunner, B.; Franks, N.; Dewanckele, J.; van Rooij, D.; Foubert, A.; Swennen, R.; Naudts, L.; Boone, M.; Cnudde, V.; Henriët, J.-P., 2010. Diagenetic formation of gypsum and dolomite in a cold-water coral mound in the Porcupine Seabight, off Ireland. *Sedimentology*, **57**: 786-805.
- Pirlet, H.; Wehrmann, L. M.; Fouberts, A.; Brunner, B.; Blamart, D.; De Mol, L.; van Rooij, D.; Dewanckele, J.; Cnudde, V.; Swennen, R.; Duyck, P.; Henriët, J.-P., 2012. Unique authigenic mineral

- assemblages reveal different diagenetic histories in two neighbouring cold-water coral mounds on Pen Duick Escarpment, Gulf of Cadiz. *Sedimentology*, **59**: 578-604.
- Raes, M.; Vanreusel, A., 2006. Microhabitat type determines the composition of nematode communities associated with sediment-clogged cold-water coral framework in the Porcupine Seabight (NE Atlantic). *Deep-Sea Research I*, **53**: 1880-1894.
- Reed, J. K., 2002. Comparison of deep-water coral reefs and lithoherms off southeastern USA. *Hydrobiologia*, **471**: 57-69.
- Reed, J. K.; Weaver, D. C.; Pomponi, S. A., 2006. Habitat and Fauna of Deep-Water *Lophelia pertusa* Coral Reefs off the Southeastern U.S.: Blake Plateau, Straits of Florida, and Gulf of Mexico. *Bulletin of marine science*, **78**: 343-375.
- Rejas, W.; Taberner, C.; De Haas, H.; Mienis, F.; Van Weering, T. C. E., 2006. Origin and Characterization of carbonate crusts of Pen Duick Escarpment (Gulf of Cadiz). *Geophysical Research Abstracts*, **8**, 07936.
- Roberts, C. M., 2002. Deep impact: the rising toll of fishing in the deep sea. *TRENDS in Ecology & Evolution*, **17**: 242-245.
- Roberts, J. M.; Long, D.; Wilson, J. B.; Mortensen, P. B.; Gage, J. D., 2003. The cold-water coral *Lophelia pertusa* (Scleractinia) and enigmatic seabed mounds along the north-east Atlantic margin: are they related? *Marine Pollution Bulletin*, **46**: 7-20.
- Roberts, S.; Hirshfield, M., 2004. Deep-sea corals: out of sight, but no longer out of mind. *Front Ecol Environ*, **2**: 123-130.
- Roberts, J. M.; Brown, C. J.; Long, D.; Bates, C. R., 2005. Acoustic mapping using a multibeam echosounder reveals cold-water coral reefs and surrounding habitats. *Coral Reefs*, **24**: 654-669.
- Roberts, J. M.; Wheeler, A. J.; Freiwald, A., 2006. Reefs of the Deep: The Biology and Geology of Cold-Water Coral Ecosystems. *Science*, **312**: 543-547.
- Rodrigues, C. L. F., 2009. Macrofaunal assemblages from mud volcanoes in the Gulf of Cadiz. PhD thesis on Marine Biology. Universidade de Aveiro, 348 pp.
- Rodrigues, C. F.; Hilário, H.; Cunha, M. R., 2012. Chemosymbiotic species from the Gulf of Cadiz (NE Atlantic): distribution, life styles and nutritional patterns. *Biogeosciences Discuss.*, **9**: 17347-17376.
- Rogers, A., 2004. The Biology, Ecology and Vulnerability of Deep-Water Coral Reefs. *International Union for Conservation of Nature & Natural Resources* (IUCN) Report. British Antarctic Survey, Cambridge. 10 pp.
- Thiem, Ø.; Ravagnan, E.; Fosså, J. H.; Berntsen, J., 2006. Food supply mechanisms for cold-water corals along a continental shelf edge. *Journal of Marine Systems*, **60**: 207-219.
- Turley, C. M.; Roberts, J. M.; Guinotte, M., 2007. Corals in deep-water: will the unseen hand of ocean acidification destroy cold-water ecosystems? *Coral Reefs*, **26**: 445-448.

- Vanreusel, A.; Andersen, A. C.; Boetius, A.; Connelly, D.; Cunha, M. R.; Decker, C.; Hilário, A.; Kormas, K. A.; Maignien, L.; Olu, K.; Pachiadaki, M.; Ritt, B.; Rodrigues, C.; Sarrazin, J.; Tyler, P.; Van Gaever, S.; Vanneste, H., 2009. Biodiversity of Cold Seep Ecosystems along the European Margins. *Oceanography*, **22**: 110-127.
- Van Rensbergen, P. V.; Depreiter, D.; Pannemans, B.; Moerkerke, G.; Van Rooij, D.; Marsset, B.; Akhmanov, G.; Blinovac, V.; Ivanov, M.; Rachidi, M.; Magalhaes, V.; Pinheiro, L.; Cunha, M.; Henriët, J.-P., 2005. The El Arraiche mud volcano field at the Moroccan Atlantic slope, Gulf of Cadiz. *Marine Geology*, **219**: 1-17.
- Van Rooij, D.; Blamart, D.; de Mol, L.; Mienis, F.; Pirlet, H.; Wehrmann, L. M.; Barbieri, R.; Maignien, L.; Templer, S. P.; de Haas, H.; Hebbeln, D.; Frank, N.; Larmagnat, S.; Stadnitskaia, A.; Stivalletta, A.; van Weering, T.; Zhang, Y.; Hamoumi, N.; Cnudde, V.; Duyck, P.; Henriët, J.-P., 2011. Cold-water coral mounds on the Pen Duick Escarpment, Gulf of Cadiz: The MICROSISTEMS project approach. *Marine Geology*, **282**: 102-117.
- Wehrmann, L. M.; Templer, S. P.; Brunner, B.; Bernasconi, S. M.; Maignien, L.; Ferdelman, T. G., 2011. The imprint of methane seepage on the geochemical record and early diagenetic processes in cold-water coral mounds on Pen Duick Escarpment, Gulf of Cadiz. *Marine Geology*, **282**: 118-137.
- Wheeler, A. J.; Beyer, A.; Freiwald, A.; de Haas, H.; Huvenne, V. A. I.; Kozachenko, M.; Olu-Le Roy, K.; Opperbecke, J., 2007. Morphology and environment of cold-water coral carbonate mounds on the NW European margin. *International Journal of Earth Sciences*, **96**: 37-56.
- Wienberg, C.; Hebbeln, D.; Fink, H. G.; Mienis, F.; Dorschel, B.; Vertino, A.; Correa, M. L.; Freiwald, A., 2009. Scleractinian cold-water corals in the Gulf of Cádiz — First clues about their spatial and temporal distribution. *Deep-Sea Research I*, **56**: 1873-1893.
- Wilson, M. V.; Shmida, A., 1984. Measuring Beta Diversity with Presence-Absence Data. *Journal of Ecology*, **72**: 1055-1064.
- Witherell, D.; Coon, C., 2001. Protecting Gorgonian Corals off Alaska from Fishing Impacts. In: Willison, J. H. M.; Hull, J.; Gass, S. E.; Kenchington, E. L. R.; Butler, M.; Doherty, P. (eds). *Proceedings of the first international symposium on deep-sea corals*. Ecology Action Centre and Nova Scotia Museum, Halifax, Nova Scotia. 117-125 pp.
- WWF (World Wide Fund for Nature), 2004. *Cold-water Corals - Fragile havens in the deep*. Oak Foundation, Boston / Geneva: 1-12. Available at <http://assets.panda.org/downloads/cwcbrochure.pdf> (last visited in November, 2011).
- Yesson, C.; Taylor, M. L.; Tittensor, D. P.; Davies, A. J.; Guinotte, J.; Baco, A.; Black, J.; Hall-Spencer, J. M.; Rogers, A. D., 2012. Global habitat suitability of cold-water octocorals. *J. Biogeogr.*, **39**: 1278-1292.
- Zitellini N.; Gràcia E.; Matias L.; Terrinha P.; Abreu M.; DeAlteriis G.; Henriët J.; Dañobeitia J.; Masson D.; Mulder T.; Ramella R.; Somoza L.; Diez S., 2009. The quest for the Africa–Eurasia plate boundary west of the Strait of Gibraltar. *Earth and Planetary Science Letters*, **208**: 13-50.



# Annexes

## Annex I

**Table I.** Sampling date, geographic location (Latitude and Longitude) and sampling depth of the sites analyzed in this study using box corer sampler during the cruises M2005 (64PE237), M2006 (64PE253) and M2007 (64PE268). The classification of each station according to the defined groups of factors analyzed in this study (Geological Feature, Depth Zone and Presence of Hard Substrate) and the analysis on which the stations were included (Quantitative or Qualitative) is also shown. Data obtained from De Haas *et al.* (2005, 2006, 2007).

Station	Date	Geographic Location		Depth	GF	HS	DZ	Analysis
		Latitude	Longitude					
M2005-01	01/06/2005	35°17.31'N	6°47.80'W	640 m	PDE	A	Z2	QL
M2005-03	21/05/2005	35°17.43'N	6°47.01'W	517 m	PDE	C	Z1	QL
M2005-04	21/05/2005	35°17.61'N	6°49.54'W	680 m	OM	A	Z3	QL
M2005-04B	21/05/2005	35°17.60'N	6°49.54'W	682 m	OM	A	Z3	QL
M2005-05A	21/05/2005	35°17.56'N	6°47.14'W	529 m	PDE	CD	Z1	QL
M2005-05B	21/05/2005	35°17.57'N	6°47.15'W	535 m	PDE	CD	Z1	QL
M2005-05C	21/05/2005	35°17.56'N	6°47.15'W	533 m	PDE	CD	Z1	QL
M2005-06A	24/05/2005	35°18.32'N	6°47.75'W	544 m	PDE	C	Z1	QL
M2005-06B	24/05/2005	35°18.33'N	6°47.75'W	546 m	PDE	C	Z1	QL
M2005-07	24/05/2005	35°18.01'N	6°47.73'W	570 m	PDE	CD	Z2	QL
M2005-10	24/05/2005	35°18.17'N	6°47.67'W	538 m	PDE	C	Z1	QL
M2005-12	25/05/2005	35°18.32'N	6°47.03'W	538 m	PDE	C	Z1	QL
M2005-13	25/05/2005	35°18.32'N	6°47.41'W	546 m	PDE	A	Z1	QL
M2005-14	25/05/2005	35°18.33'N	6°47.72'W	546 m	PDE	C	Z1	QL
M2005-15	25/05/2005	35°18.33'N	6°47.93'W	570 m	PDE	C	Z2	QL
M2005-16A	26/05/2005	35°18.31'N	6°48.21'W	660 m	PDE	C	Z3	QL
M2005-16B	26/05/2005	35°18.30'N	6°48.21'W	665 m	PDE	C	Z3	QL
M2005-17	26/05/2005	35°18.32'N	6°48.12'W	618 m	PDE	CD	Z2	QL
M2005-19A	30/05/2005	35°18.92'N	6°46.84'W	547 m	OM	A	Z1	QL
M2005-20	30/05/2005	35°18.99'N	6°46.65'W	516 m	LMV	-	-	QL
M2005-20	30/05/2005	35°18.99'N	6°46.65'W	516 m	LMV	-	-	QL
M2005-21	30/05/2005	35°19.08'N	6°46.40'W	498 m	LMV	-	-	QL
M2005-22	30/05/2005	35°19.11'N	6°46.26'W	518 m	LMV	-	-	QL
M2005-23	30/05/2005	35°19.19'N	6°46.03'W	559 m	OM	C	Z1	QL
M2005-28A	31/05/2005	35°18.20'N	6°48.53'W	622 m	PDE	C	Z2	QL

Table I. Continued.

Station	Date	Geographic Location		Depth	GF	HS	DZ	Analysis
		Latitude	Longitude					
M2005-28B	31/05/2005	35°18.20'N	6°48.53'W	622 m	PDE	C	Z2	QL
M2005-29A	01/06/2005	35°18.44'N	6°48.54'W	628 m	PDE	A	Z2	QL
M2005-29B	01/06/2005	35°18.43'N	6°48.54'W	628 m	PDE	A	Z2	QL
M2005-30A	01/06/2005	35°18.76'N	6°47.86'W	556 m	PDE	CD	Z1	QL
M2005-30B	01/06/2005	35°18.76'N	6°47.90'W	550 m	PDE	CD	Z1	QL
M2005-31	01/06/2005	35°18.79'N	6°47.93'W	559 m	PDE	C	Z1	QL
M2006-06	06/10/2006	35°16.88'N	6°45.35'W	418 m	GMV	-	-	QL+Q
M2006-08	07/10/2006	35°16.75'N	6°45.72'W	444 m	GMV	-	-	QL+Q
M2006-09	07/10/2006	35°16.76'N	6°45.76'W	451 m	GMV	-	-	QL+Q
M2006-10	07/10/2006	35°16.83'N	6°45.54'W	432 m	GMV	-	-	QL+Q
M2006-11	07/10/2006	35°16.79'N	6°45.59'W	438 m	GMV	-	-	QL+Q
M2006-13	08/10/2006	35°16.65'N	6°46.11'W	516 m	OM	CD	Z1	QL+Q
M2006-14	08/10/2006	35°16.58'N	6°46.37'W	575 m	OM	A	Z2	QL+Q
M2006-15	08/10/2006	35°16.54'N	6°46.47'W	600 m	OM	CD	Z2	QL+Q
M2006-17	08/10/2006	35°16.29'N	6°46.93'W	612 m	OM	A	Z2	QL+Q
M2006-18	08/10/2006	35°16.39'N	6°46.40'W	608 m	OM	C	Z2	QL+Q
M2006-19	09/10/2006	35°11.31'N	7°04.30'W	908 m	OM	CD	Z3	QL+Q
M2006-21	10/10/2006	35°19.00'N	6°48.05'W	560 m	PDE	CD	Z2	QL+Q
M2006-22	10/10/2006	35°19.00'N	6°48.16'W	557 m	PDE	C	Z1	QL+Q
M2006-23	10/10/2006	35°19.02'N	6°48.22'W	557 m	PDE	C	Z1	QL+Q
M2006-24	10/10/2006	35°19.02'N	6°48.34'W	571 m	PDE	C	Z2	QL+Q
M2006-25	10/10/2006	35°19.00'N	6°48.56'W	648 m	PDE	CD	Z3	QL+Q
M2006-26	10/10/2006	35°19.00'N	6°48.65'W	628 m	PDE	CD	Z2	QL+Q
M2006-27	10/10/2006	35°19.00'N	6°48.85'W	622 m	PDE	A	Z2	QL+Q
M2006-28	10/10/2006	35°19.01'N	6°49.00'W	642 m	PDE	CD	Z3	QL+Q
M2006-30	11/10/2006	35°19.00'N	6°49.27'W	651 m	PDE	C	Z3	QL+Q
M2006-31	11/10/2006	35°19.00'N	6°49.68'W	671 m	PDE	C	Z3	QL+Q
M2006-33	11/10/2006	35°18.93'N	6°47.59'W	542 m	PDE	CD	Z1	QL+Q
M2006-34	11/10/2006	35°18.92'N	6°47.41'W	542 m	PDE	C	Z1	QL+Q
M2006-35	11/10/2006	35°18.92'N	6°47.21'W	542 m	PDE	C	Z1	QL+Q
M2006-36	12/10/2006	35°18.92'N	6°46.97'W	542 m	PDE	C	Z1	QL+Q
M2006-38A	12/10/2006	35°19.09'N	6°46.40'W	494 m	LMV	-	-	QL
M2006-38B	12/10/2006	35°19.09'N	6°46.40'W	497 m	LMV	-	-	QL+Q

Table I. Continued.

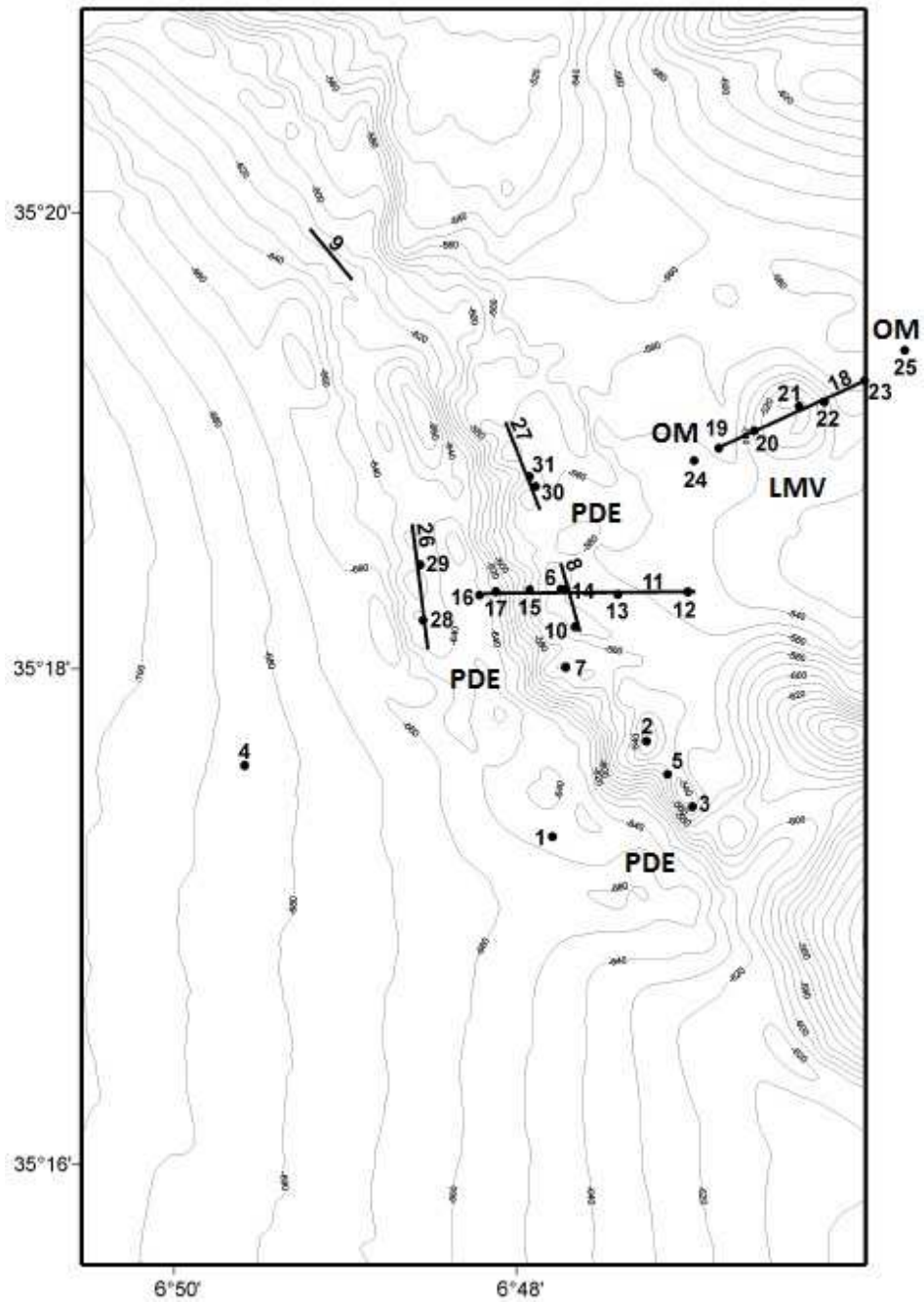
Station	Date	Geographic Location		Depth	GF	HS	DZ	Analysis
		Latitude	Longitude					
M2006-38C	12/10/2006	35°19.09'N	6°46.40'W	497 m	LMV	-	-	QL
M2006-38D	12/10/2006	35°19.09'N	6°46.40'W	497 m	LMV	-	-	QL
M2006-38F	12/10/2006	35°19.09'N	6°46.40'W	497 m	LMV	-	-	QL
M2006-39	13/10/2006	35°18.90'N	6°47.90'W	560 m	PDE	C	Z2	QL+Q
M2006-40	13/10/2006	35°18.90'N	6°47.02'W	542 m	PDE	C	Z1	QL
M2006-40A	13/10/2006	35°18.91'N	6°47.03'W	560 m	PDE	C	Z1	QL
M2006-41	13/10/2006	35°18.91'N	6°48.18'W	568 m	PDE	C	Z2	QL+Q
M2006-42	13/10/2006	35°18.92'N	6°48.39'W	637 m	PDE	C	Z2	QL+Q
M2006-44	13/10/2006	35°18.90'N	6°48.90'W	640 m	PDE	C	Z2	QL
M2006-44A	13/10/2006	35°18.90'N	6°48.90'W	640 m	PDE	C	Z2	QL+Q
M2006-46A	14/10/2006	35°13.86'N	6°36.60'W	228 m	AMV	-	-	QL
M2006-46B	14/10/2006	35°13.85'N	6°36.59'W	227 m	AMV	-	-	QL+Q
M2006-48	14/10/2006	35°17.90'N	6°39.00'W	376 m	MMV	-	-	QL+Q
M2006-49	14/10/2006	35°17.90'N	6°38.64'W	360 m	MMV	-	-	QL+Q
M2006-51	15/10/2006	35°18.57'N	6°48.28'W	624 m	PDE	CD	Z2	QL+Q
M2006-52	15/10/2006	35°18.43'N	6°48.23'W	622 m	PDE	CD	Z2	QL+Q
M2006-53	15/10/2006	35°18.31'N	6°48.20'W	651 m	PDE	CD	Z2	QL+Q
M2006-54	15/10/2006	35°18.09'N	6°48.12'W	634 m	PDE	C	Z2	QL+Q
M2006-56	15/10/2006	35°17.99'N	6°48.03'W	622 m	PDE	CD	Z2	QL+Q
M2006-57	16/10/2006	35°17.92'N	6°47.94'W	598 m	PDE	C	Z2	QL+Q
M2006-58	16/10/2006	35°17.86'N	6°47.88'W	606 m	PDE	C	Z2	QL+Q
M2006-59	16/10/2006	35°17.79'N	6°47.77'W	637 m	PDE	C	Z2	QL+Q
M2007-04	01/05/2007	35°14.00'N	6°46.04'W	597 m	OM	A	Z2	QL+Q
M2007-05	01/05/2007	35°14.01'N	6°45.49'W	581 m	OM	C	Z2	QL+Q
M2007-07	01/05/2007	35°14.62'N	6°37.98'W	432 m	OM	A	Z1	QL+Q
M2007-09	02/05/2007	35°14.04'N	6°37.94'W	428 m	OM	C	Z1	QL+Q
M2007-11	02/05/2007	35°18.03'N	6°44.52'W	493 m	M	C	Z1	QL
M2007-11A	02/05/2007	35°17.99'N	6°44.48'W	489 m	M	C	Z1	QL+Q
M2007-12	03/05/2007	35°18.04'N	6°44.51'W	500 m	M	U	Z1	QL
M2007-13A	03/05/2007	35°18.00'N	6°44.49'W	475 m	M	C	Z1	QL+Q

Table I. Continued.

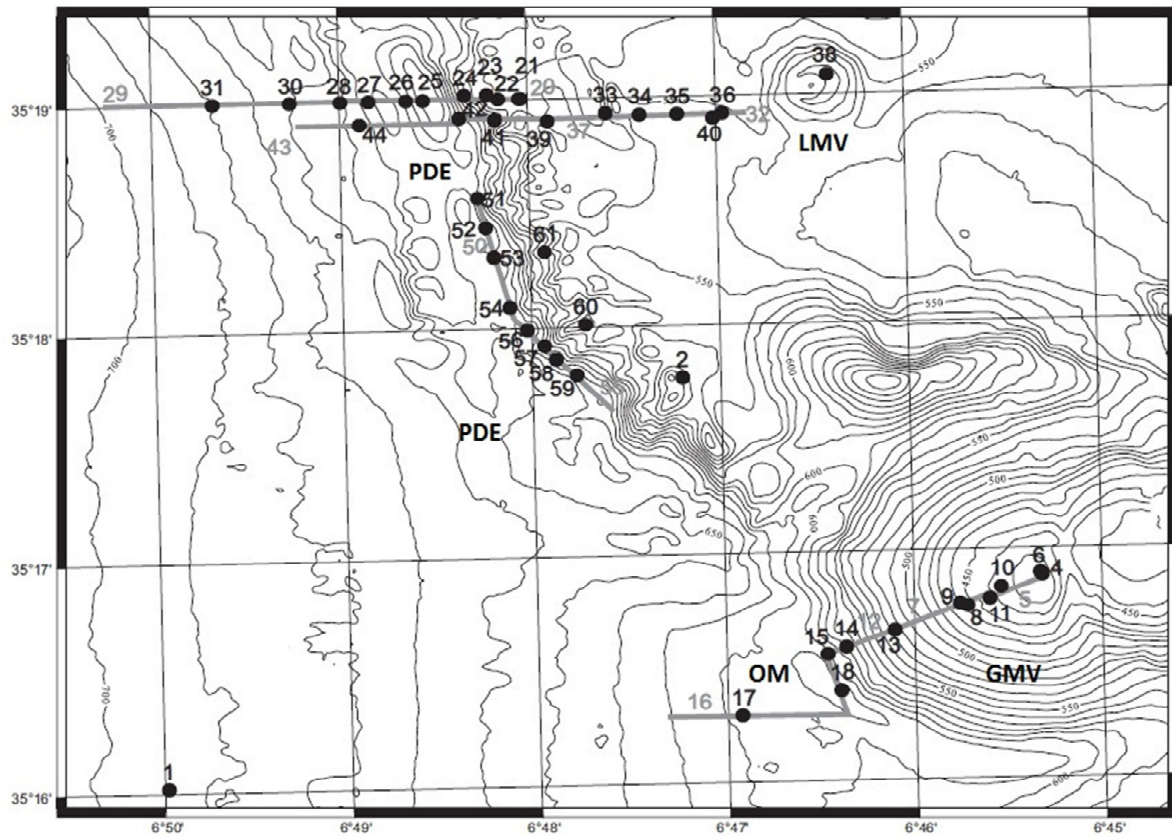
Station	Date	Geographic Location		Depth	GF	HS	DZ	Analysis
		Latitude	Longitude					
M2007-13B	03/05/2007	35°18.01'N	6°44.49'W	493 m	M	C	Z1	QL+Q
M2007-15	04/05/2007	35°17.91'N	6°44.29'W	444 m	M	C	Z1	QL
M2007-16	04/05/2007	35°17.61'N	6°43.61'W	473 m	M	C	Z1	QL
M2007-17	04/05/2007	35°17.06'N	6°42.62'W	416 m	M	CD	Z1	QL+Q
M2007-18A	15/05/2007	35°09.90'N	6°46.39'W	740 m	M	A	Z3	QL
M2007-18B	15/05/2007	35°09.90'N	6°46.39'W	742 m	M	A	Z3	QL
M2007-19	05/05/2007	35°16.92'N	6°45.47'W	430 m	GMV	-	-	QL+Q
M2007-20	05/05/2007	35°16.99'N	6°53.29'W	765 m	OM	A	Z3	QL+Q
M2007-23	06/05/2007	35°17.77'N	6°43.96'W	498 m	M	A	Z1	QL
M2007-24	06/05/2007	35°17.73'N	6°43.89'W	495 m	M	C	Z1	QL+Q
M2007-25	06/05/2007	35°17.70'N	6°43.80'W	490 m	M	C	Z1	QL+Q
M2007-26	06/05/2007	35°17.66'N	6°43.72'W	485 m	M	CD	Z1	QL+Q
M2007-27	06/05/2007	35°17.63'N	6°43.64'W	471 m	M	C	Z1	QL+Q
M2007-28	06/05/2007	35°17.59'N	6°43.55'W	515 m	M	C	Z1	QL
M2007-29	06/05/2007	35°17.55'N	6°43.47'W	508 m	M	C	Z1	QL
M2007-36	11/05/2007	34°59.89'N	6°44.61'W	465 m	M	A	Z1	QL+Q
M2007-37	11/05/2007	35°00.06'N	6°44.76'W	478 m	M	U	Z1	QL+Q
M2007-39	11/05/2007	35°00.23'N	6°44.89'W	441 m	M	A	Z1	QL
M2007-40	12/05/2007	35°00.14'N	6°44.81'W	473 m	M	U	Z1	QL
M2007-41	12/05/2007	35°00.11'N	6°44.82'W	461 m	M	U	Z1	QL
M2007-42	12/05/2007	35°00.06'N	6°44.94'W	451 m	M	C	Z1	QL
M2007-45	13/05/2007	35°01.01'N	6°59.06'W	800 m	M	C	Z3	QL
M2007-46	13/05/2007	35°01.18'N	6°58.89'W	720 m	M	U	Z3	QL+Q
M2007-50	14/05/2007	35°01.34'N	6°58.90'W	740 m	M	C	Z3	QL
M2007-51	14/05/2007	35°01.29'N	6°59.02'W	740 m	M	U	Z3	QL
M2007-53	15/05/2007	35°10.29'N	6°47.28'W	750 m	M	U	Z3	QL
M2007-54	15/05/2007	35°10.23'N	6°47.30'W	750 m	M	U	Z3	QL+Q
M2007-55	15/05/2007	35°10.00'N	6°47.37'W	700 m	M	U	Z3	QL+Q

GF: Geological feature; AMV: Al Idrissi mud volcano; GMV: Gemini mud volcano; LMV: Lazarillo de Tormes mud volcano; MMV: Mercator mud volcano; M: mound; OM: off mound; PDE: Pen Duick Escarpment; HS: Hard substrate; C: coral at surface; CD: coral at sediment subsurface; A: absence of coral; U: Undetermined (excluded from HS analysis); DZ: Depth zone; Z1: depth zone 1 (sites at < 560 m depth corresponding to the top of the scarp); Z2: depth zone 2 (sites at 560-640 m depth, corresponding to the scarp); Z3: depth zone 3 (sites at > 640 m depth, corresponding to the base of the scarp); -: exclusion of MV samples from the analysis; QL: Qualitative analysis; Q: Quantitative analysis.

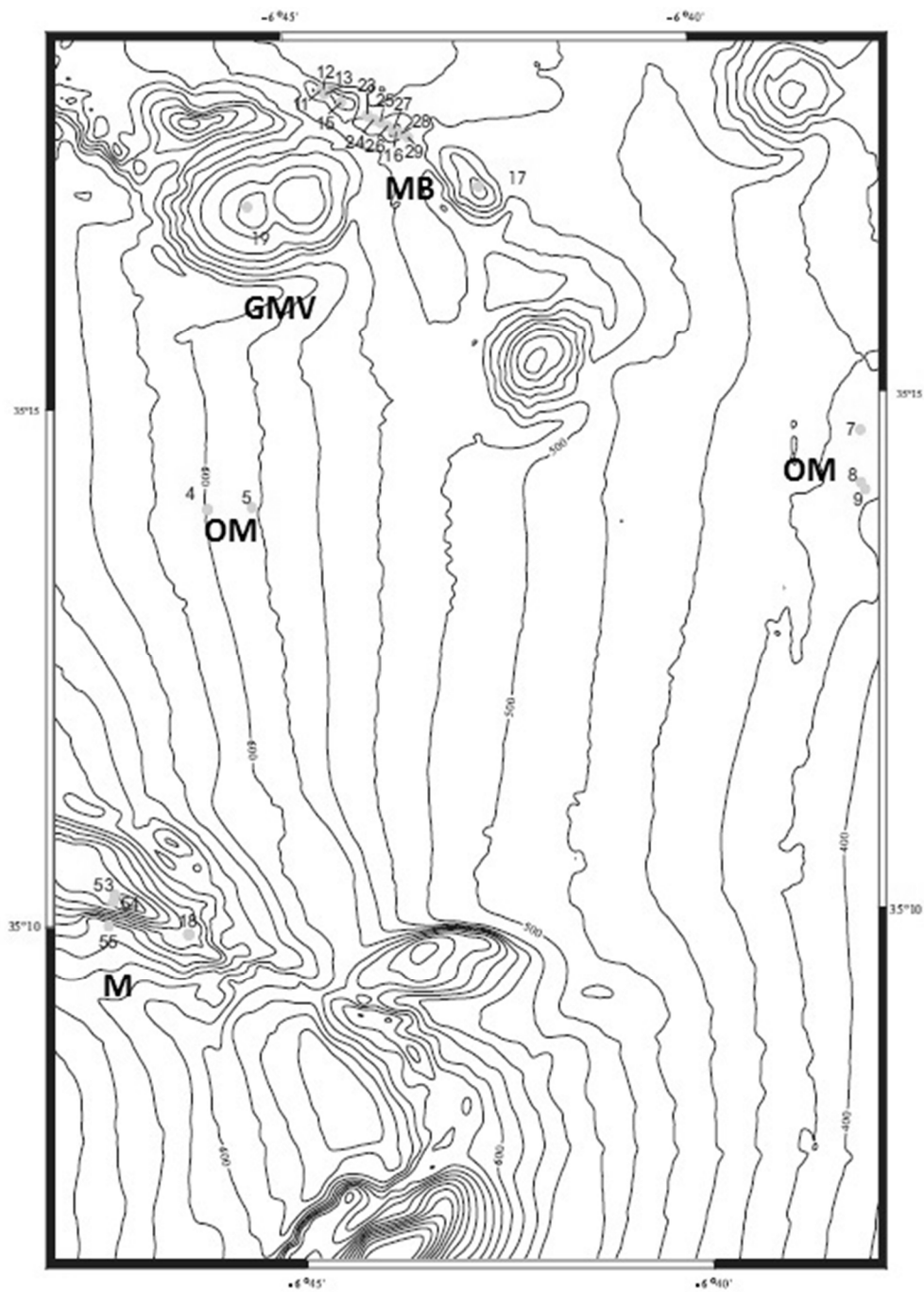
## Annex II



**Figure 1.** Stations and hopper camera lines at Pen Duick Escarpment (PDE) sampled during the cruise M2005 (64PE237). Not all the stations correspond to box-corer samples thus not considered for this study. LMV: Lazarillo de Tormes mud volcano; OM: off mound areas. Adapted and modified from De Haas *et al.* (2005).



**Figure 2.** Map with some of the stations sampled at the Pen Duick Escarpment (PDE) and surrounding areas during the cruise M2006 (64PE253). GMV: Gemini mud volcano; LMV: Lazarillo de Tormes mud volcano; OM: off mound areas. Adapted and modified from De Haas *et al.* (2006).



**Figure 3.** Map with some of the box-core stations sampled at the El Arraiche field during the cruise M2007 (64PE268). GMV: Gemini mud volcano; M: mound areas; MB: mound B; OM: off mound areas; PDE: Pen Duick Escarpment. Adapted and modified from De Haas *et al.* (2007).



## Annex III

Preliminary list of taxa of macrofauna found in the Gulf of Cadiz area. Taxonomic data in accordance to WoRMS – *World Register of Marine Species* (<http://www.marinespecies.org>). Taxonomic order of major groups according to Brusca & Brusca (2003) and Rouse and Pleijel (2001).

Brusca, R. C.; Brusca, G. J., 2003. Invertebrates (2nd ed). Sinauer Associates, Sunderland, MA.

Rouse, G. W.; Pleijel, F., 2001. Polychaetes. Oxford University Press, Oxford.

### Kingdom ANIMALIA

Phylum PORIFERA Grant, 1836

Porifera undetermined

Phylum CNIDARIA Verrill, 1865

Cnidaria undetermined

Class Hydrozoa Owen, 1843

Hydrozoa undetermined

Order Leptothecata Cornelius, 1992

Family Aglaopheniidae Marktanner-Turneretscher, 1890

Genus *Aglaophenia* Lamouroux, 1812

***Aglaophenia lophocarpa*** Allman, 1877

Genus *Cladocarpus* Allman, 1874

***Cladocarpus sinuosus*** Vervoort, 1966

Genus *Lytocarpia* Kirchenpauer, 1872

***Lytocarpia myriophyllum*** (Linnaeus, 1758)

Genus *Streptocaulus* Allman, 1883

***Streptocaulus dollfusi*** (Billard, 1924)

Family Campanulariidae Johnston, 1836

Genus *Clytia* Lamouroux, 1812

***Clytia linearis*** (Thorneley, 1900)

Family Campanulinidae Hincks, 1868

Genus *Campanulina* Van Beneden, 1847

Cryptic ***Campanulina panicula sp1/2*** G.O. Sars, 1874 (as in Moura, 2011)

Genus *Lafoeina* Sars, 1869

***Lafoeina tenuis*** Sars, 1874

Family Halopterididae Millard, 1962

Genus *Antennella* Allman, 1877

***Antennella secundaria*** (Gmelin, 1791)

Family Lafoeidae Hincks, 1868

***Lafoeidae sp.***

Genus *Acryptolaria* Norman, 1875

***Acryptolaria cf. conferta*** (Allman, 1877)

***Acryptolaria cf. flabellum*** (Allman, 1888)

Genus *Cryptolaria* Busk, 1857

***Cryptolaria pectinata*** (Allman, 1888)

Genus *Filellum* Hincks, 1869

***Filellum sp.***

***Filellum cf. serratum*** (Clarke, 1879)

Genus *Lafoea* Lamouroux, 1821

Cryptic ***Lafoea cf. dumosa sp3*** (Fleming, 1820) (as in Moura *et al.*, 2011)

Genus *Zygophylax* Quelch, 1885

***Zygophylax sp.***

***Zygophylax biarmata*** Billard, 1905

***Zygophylax brownei*** Billard, 1924

***Zygothylax levinseni*** (Saemundsson, 1911)

Family Lovenellidae Russell, 1953

Genus *Lovenella* Hincks, 1868

***Lovenella producta*** (Sars G.O., 1874)

Family Plumulariidae Agassiz, 1862

Plumulariidae sp2

Genus *Nemertesia* Lamouroux, 1812

Cryptic ***Nemertesia cf. antennina*** (Linnaeus, 1758) (as in Moura *et al.*, 2012)

***Nemertesia ventriculiformis*** (Marktanner-Turneretscher, 1890)

Genus *Polyplumaria* Sars, 1874

***Polyplumaria flabellata*** Sars, 1874

Family Sertulariidae Lamouroux, 1812

Genus *Sertularella* Gray, 1848

***Sertularella robusta*** Coughtrey, 1876

Family Tiarannidae Russell, 1940

Genus *Modeeria* Forbes, 1848

***Modeeria rotunda*** (Quoy & Gaimard, 1827)

**Class Anthozoa** Ehrenberg, 1834

**Anthozoa undetermined**

**Subclass Hexacorallia** Haeckel, 1896

Order Antipatharia

**Antipatharia undetermined**

Order Zoantharia Gray, 1832

Family Parazoanthidae Delage & Hérouard, 1901

Genus *Parazoanthus* Haddon & Shackleton, 1891

***Parazoanthus sp.***

**Subclass Octocorallia**

Order Alcyonacea Lamouroux, 1812

Family Alcyoniidae Lamouroux, 1812

Genus *Anthomastus* Verrill, 1878

***Anthomastus sp.***

Family Anthothelidae Broch, 1916

Genus *Anthothela* Verrill, 1879

***Anthothela cf. grandiflora*** (M. Sars, 1856)

Family Isididae Lamouroux, 1812

Genus *Isidella* Gray, 1857

***Isidella elongata*** (Esper, 1788)

Family Plexauridae Gray, 1859

***cf. Plexauridae sp.***

Genus *Paramuricea* Koelliker, 1865

***Paramuricea sp.***

Order Pennatulacea Verrill, 1865

**Pennatulacea undetermined**

Family Pennatulidae Ehrenberg, 1834

Genus *Pennatula* Linnaeus, 1758

***Pennatula phosphorea*** Linnaeus, 1758

Family Virgulariidae Verrill, 1868

Genus *Virgularia* Lamarck, 1816

***Virgularia mirabilis*** (Müller, 1776)

**Class Scyphozoa** Götte, 1887

Order Coronatae

Family Nausithoidae (Claus, 1883)

Genus *Nausithoe* Kölliker, 1853

***Nausithoe sp.***

**Phylum NEMERTEA**

- Nemertea undetermined**
- Phylum CEPHALORHYNCHA**  
 Class Priapulida Théel, 1906  
**Priapulida undetermined (several species)**
- Phylum SIPUNCULA**  
**Sipuncula undetermined (several species)**
- Phylum ECHIURA**  
**Echiura undetermined (several species)**
- Phylum ANNELIDA**  
 Class Polychaeta Grube 1850  
 Subclass Sedentaria Lamarck, 1818  
 Infraclass Scolecida Rouse & Fauchald, 1997 non Linnaean
- Order Capitellida  
 Family Capitellidae Grube, 1862  
**Capitellidae undetermined**  
**Capitellidae sp1**  
 Genus *Notomastus* Sars, 1850  
**cf. *Notomastus* sp.**  
 Family Maldanidae Malmgren, 1867  
**Maldanidae spp.**
- Order Opheliida  
 Family Opheliidae Malmgren, 1867  
**Opheliidae und**  
 Genus *Ophelina* Örsted, 1843  
***Ophelina abranchiata* Støp-Bowitz, 1948**  
***Ophelina acuminata* Örsted, 1843**  
***Ophelina cf. cylindricaudata* (Hansen, 1879)**  
 Family Scalibregmatidae Malmgren, 1867  
 Genus *Asclerocheilus* Ashworth, 1901  
***Asclerocheilus intermedius* (Saint-Joseph, 1894)**  
 Genus *Axiokebuita* Pocklington & Fournier, 1987  
**cf. *Axiokebuita* sp.**
- Order Orbiniida  
 Family Orbiniidae Hartman, 1942  
 Genus *Leitoscoloplos* Day, 1977  
**cf. *Leitoscoloplos* sp.**  
 Genus *Scoloplella* Day, 1963  
**cf. *Scolophella* sp.**  
 Family Paraonidae Cerruti, 1909  
**Paraonidae undetermined**  
 Genus *Paradoneis* Hartman, 1965  
***Paradoneis* spp.**  
 Genus *Levinsenia* Mesnil, 1897  
***Levinsenia* spp.**  
 Genus *Aricidea* Webster, 1879  
***Aricidea* spp. (4 species)**  
 Family Cossuridae Day, 1963  
**Cossuridae und**
- Infraclass Canalipalata Rouse & Fauchald, 1997 non Linnaean**
- Order Sabellida  
 Family Siboglinidae Caullery, 1914  
 Genus *Siboglinum* Caullery, 1914  
***Siboglinum* spp.**  
 Family Sabellariidae Johnston, 1865  
 Genus *Gesaia* Kirtley, 1994

- Gesaia elegans*** (Fauvel, 1911)  
 Genus *Tetreres* Caullery, 1913  
***Tetreres cf. baileyae*** Kirtley, 1994  
 Family Oweniidae Rioja, 1917  
 Genus *Myriochele* Malmgren, 1867  
***Myriochele danielsseni*** Hansen, 1878  
 Family Sabellidae Latreille, 1825  
**Sabellidae spp. (several species)**  
 Genus *Euchone* Malmgren, 1866  
***Euchone* sp.**  
 Family Serpulidae Rafinesque, 1815  
**Serpulidae sp.**
- Order Terebellida sensu Rouse & Fauchald, 1997
- Suborder Cirratuliformia**  
 Family Cirratulidae Carus, 1863  
**cf. Cirratulidae undetermined**  
 Genus *Chaetozone* Malmgren, 1867  
***Chaetozone* sp.**  
 Genus *Dodecaceria* Örsted, 1843  
***Dodecaceria cf. concharum*** Örsted, 1843  
 Family Fauveliopsidae Hartman, 1971  
 Genus *Laubieriopsis* Petersen, 2000  
***Laubieriopsis brevis*** (Hartman, 1967)  
***Laubieriopsis cabiochi*** (Amoureux, 1982)  
 Family Flabelligeridae de Saint-Joseph, 1894  
**Flabelligeridae spp. (3 species)**
- Suborder Terebellomorpha**  
 Family Ampharetidae Malmgren, 1866  
**Ampharetidae spp. (2 species)**  
 Genus *Ampharete* Malmgren, 1866  
***Ampharete* sp.**  
 Genus *Amphicteis* Grube, 1850  
***Amphicteis* sp.**  
 Genus *Melinnopsides* Day, 1964  
**cf. *Melinnopsides* sp.**  
 Genus *Samythella* Verrill, 1873  
***Samythella* sp.**  
 Family Terebellidae Johnston, 1846  
**Terebellidae undetermined**  
 Genus *Pista* Malmgren, 1866  
***Pista cf. cristata*** (Müller, 1776)  
 Family Trichobranchidae Malmgren, 1866  
 Genus *Terebellides* Sars, 1835  
***Terebellides atlantis*** Williams, 1984
- Order Spionida sensu Rouse & Fauchald, 1997  
 Family Chaetopteridae Audouin & Milne Edwards, 1833  
 Genus *Spiochaetopterus* Sars, 1853  
***Spiochaetopterus bergensis*** Gitay, 1969 / *S. typicus* M. Sars, 1856  
 Family Magelonidae Cunningham & Ramage, 1888  
 Genus *Magelona* F. Müller, 1858  
***Magelona* sp.**  
 Family Poecilochaetidae Hannerz, 1956  
 Genus *Poecilochaetus* Claparède, 1875  
***Poecilochaetus cf. serpens*** Allen, 1904  
 Family Spionidae Grube, 1850

**Spionidae undetermined**Genus *Polydora* Bosc, 1802***Polydora* sp.**Genus *Prionospio* Malmgren, 1867***Prionospio* spp.**Genus *Spiophanes* Grube, 1860***Spiophanes* sp.****Subclass Errantia Audouin & Milne-Edwards, 1832**

Order Phyllodocida Dales, 1962

**Suborder Aphroditiformia Levinsen, 1883**

Family Polynoidae Malmgren, 1867

**Polynoidae spp. (2 species)**Genus *Anotochaetonoe***cf. *Anotochaetonoe* sp.**Genus *Harmothoe* Kinberg, 1856***Harmothoe* cf. *evei* Kirkegaard, 1980**Genus *Robertianella* McIntosh, 1885**cf. *Robertianella* sp.**Genus *Subadyte* Pettibone, 1969***Subadyte pellucida* (Ehlers, 1864)**

Family Sigalionidae Malmgren, 1867

Genus *Fimbriosthenelais* Pettibone, 1971***Fimbriosthenelais zetlandica* (McIntosh, 1876)**Genus *Pholoides* Pruvot, 1895***Pholoides dorsipapillatus* (Marenzeller, 1893)****Suborder Nereidiformia**

Family Nereididae Blainville, 1818

Genus *Sinonereis* Wu & Sun, 1979***Sinonereis* cf. *heteropoda* Wu & Sun, 1979**

Family Syllidae Grube, 1850

**Syllidae undetermined**

Subfamily Eusyllinae Malaquin, 1893

**Eusyllinae undetermined**

Subfamily Exogoninae Langerhans, 1879

**Exogoninae undetermined**

Subfamily Syllinae Rioja, 1925

**Syllinae undetermined**

Family Hesionidae Grube, 1850

**Hesionidae undetermined**Genus *Leocrates* Kinberg, 1866***Leocrates atlanticus* (McIntosh, 1885)**

Family Pilargidae de Saint-Joseph, 1899

**Pilargidae spp. (2 species)**Genus *Ancistrostylis* McIntosh, 1879***Ancistrostylis* sp.**Genus *Synelmis* Chamberlin, 1919**cf. *Synelmis* sp.****Suborder Glyceriformia****Glyceriformia undetermined**

Family Glyceridae Grube, 1850

Genus *Glycera* Savigny, 1818***Glycera lapidum* Quatrefages, 1866*****Glycera* cf. *unicornis* Savigny in Lamarck, 1818**Genus *Glycerella* Arwidsson, 1899***Glycerella magellanica* (McIntosh, 1885)**

Family Goniadidae Kinberg, 1866

**Goniadidae sp1**

**Suborder Phyllodocida incertae sedis**

Family Nephtyidae Grube, 1850

**Nephtyidae undetermined**

Genus *Aglaophamus* Kinberg, 1865

***Aglaophamus elamellatus*** (Eliason, 1951)

***Aglaophamus pulcher*** (Rainer, 1991)

Genus *Micronephthys* Friedrich, 1939

***Micronephthys cf. minuta*** (Théel, 1879)

Genus *Nephtys* Cuvier, 1817

***Nephtys hystricis*** McIntosh, 1900

***Nephtys paradoxa*** Malm, 1874

**Suborder Phyllodociformia Levinsen, 1883**

Family Phyllodocidae Örsted, 1843

**Phyllodocidae undetermined**

Genus *Phyllodoce* Lamarck, 1818

***Phyllodoce lineata*** (Claparède, 1870)

***Phyllodoce madeirensis*** Langerhans, 1880

Order Amphinomida

Family Amphinomidae Savigny in Lamarck, 1818

Genus *Chloenopsis* Fauchald, 1977

***Chloenopsis atlantica*** (McIntosh, 1885)

Order Eunicida

Family Eunicidae Berthold, 1827

**Eunicidae undetermined**

Genus *Eunice* Cuvier, 1817

***Eunice cf. dubitata*** Fauchald, 1974

***Eunice cf. vittata*** (Delle Chiaje, 1828)

Genus *Lysidice* Lamarck, 1818

***Lysidice ninetta*** Audouin & Milne-Edwards, 1833

***Lysidice unicornis*** (Grube, 1840)

Genus *Marphysa* Quatrefages, 1865

***Marphysa bellii*** (Audouin & Milne-Edwards, 1833)

Family Lumbrineridae Schmarda, 1861

**Lumbrineridae undetermined**

Genus *Lumbrinerides* Orensanz, 1973

**cf. *Lumbrinerides* sp.**

Genus *Lumbrineris* Blainville, 1828

**cf. *Lumbrineris* spp. (3 species)**

Genus *Augeneria* Monro, 1930

**cf. *Augeneria* sp.**

Family Onuphidae Kinberg, 1865

Genus *Aponuphis* Kucheruk, 1978

***Aponuphis cf. bilineata*** (Baird, 1870)

Genus *Hyalinoecia* Malmgren, 1867

***Hyalinoecia tubicola*** (O.F. Müller, 1776)

Genus *Paradiopatra* Ehlers, 1887

***Paradiopatra cf. hispanica*** (Amoureux, 1972)

Family Oeononidae Kinberg, 1865

**Oeononidae undetermined**

Family Dorvilleidae Chamberlin, 1919

**Dorvilleidae undetermined**

**Class Clitellata**

**Subclass Oligochaeta**

**Oligochaeta undetermined****Phylum ARTHROPODA****Subphylum Crustacea****Crustacea undetermined**

Class Malacostraca Latreille, 1802

Superorder Leptostraca Claus, 1880

Order Nebaliacea Calman, 1904

**Nebaliacea sp1**

Superorder Eucarida Calman, 1904

Order Decapoda

**Infraorder Caridea Dana, 1852**

Family Alpheidae Rafinesque, 1815

Genus *Alpheus* Fabricius, 1798***Alpheus* sp.**

Family Pandalidae Haworth, 1825

**cf. Pandalidae undetermined**

Family Processidae Ortmann, 1896

Genus *Processa* Leach, 1815 [in Leach, 1815-1875]***Processa* cf. *elegantula* Nouvel & Holthuis, 1957****Infraorder Brachyura Linnaeus, 1758**

Family Cymonomidae Bouvier, 1898

Genus *Cymonomus* A. Milne-Edwards, 1880***Cymonomus granulatus* (Norman, in Thomson, 1873)**

Family Leucosiidae Samouelle, 1819

Genus *Ebalia* Leach, 1817***Ebalia nux* A. Milne-Edwards, 1883**

Family Polybiidae Ortmann, 1893

Genus *Bathynectes* Stimpson, 1871***Bathynectes maravigna* (Prestandrea, 1839)**

Family Xanthidae MacLeay, 1838

Genus *Monodaeus* Guinot, 1967***Monodaeus couchii* (Couch, 1851)****Infraorder Anomura MacLeay, 1838**

Family Munididae Ah Yong, Baba, Macpherson, Poore, 2010

Genus *Munida* Leach, 1820***Munida intermedia* A. Milne Edwards & Bouvier, 1899 / *M. sarsi* Huus, 1935**

Order Euphausiacea Dana, 1850

Family Euphausiidae Dana, 1852

Genus *Euphausia* Dana, 1850***Euphausia hemigibba* Hansen, 1910**

Superorder Peracarida Calman, 1904

Order Mysida Boas, 1883

**Mysida undetermined**

Family Mysidae Haworth, 1825

**Mysidae undetermined**Genus *Erythrops* G.O. Sars, 1869***Erythrops* sp1*****Erythrops neapolitana* Colosi, 1929**Genus *Paramblyops* Holt & Tattersall, 1905***Paramblyops rostratus* Holt & Tattersall, 1905**Genus *Parerythrops* G.O. Sars, 1869**cf. *Parerythrops* sp.**Genus *Pseudomma* G.O. Sars, 1870***Pseudomma* sp1*****Pseudomma affine* G.O. Sars, 1870**

Order Cumacea Krøyer, 1846

**Cumacea undetermined**

Family Bodotriidae T. scott, 1901

**Bodotriidae undetermined**

Subfamily Vaunthompsoniinae

**Vaunthompsoniinae und**

Genus *Vaunthompsonia* Bate, 1858

***Vaunthompsonia cf. cristata* Bate, 1858**

Family Diastylidae Bate, 1856

**Diastylidae undetermined**

Genus *Diastylis* Say, 1818

***Diastylis* spp. (several species)**

Genus *Diastylodes* G.O. Sars, 1900

***Diastylodes* sp.**

***Diastylodes aff. biplicatus* (Sars G.O., 1865)**

Genus *Diastylopsis* Smith, 1880

**cf. *Diastylopsis* sp.**

Genus *Leptostylis* G.O. Sars, 1869

**cf. *Leptostylis* sp.**

Family Lampropidae Sars, 1878

**Lampropidae undetermined**

Genus *Hemilamprops* G.O. Sars, 1883

***Hemilamprops cf. cristatus* (Sars G.O., 1870)**

Genus *Platysympus* Stebbing, 1912

***Platysympus typicus* (Sars, 1870)**

Family Leuconidae Sars, 1878

**Leuconidae spp. (several species)**

Genus *Leucon* (*Leucon*) Krøyer, 1846

***Leucon (Leucon) cf. nasicoides* (Krøyer, 1841)**

Genus *Eudorella* Norman, 1867

***Eudorella emarginata* (Krøyer, 1846)**

Family Nannastacidae Bate, 1866

**Nannastacidae sp1**

Genus *Campylaspis* G.O. Sars, 1865

***Campylaspis* sp1**

***Campylaspis aff. affinis* Sars, 1870**

***Campylaspis aff. glabra* Sars, 1878**

***Campylaspis glabra* Sars, 1878**

***Campylaspis aff. horrida* Sars, 1870**

***Campylaspis sulcata* Sars, 1870**

Genus *Procampylaspis* Bonnier, 1896

**cf. *Procampylaspis* sp.**

Genus *Nannastacus* Bate, 1865

***Nannastacus* spp.**

Order Tanaidacea Dana, 1849

**Suborder Apseudomorpha Sieg, 1980**

Family Apseudidae Leach, 1814

**Apseudidae undetermined**

Subfamily Apseudinae Leach, 1814

Genus *Apseudes* Leach, 1813

***Apseudes grossimanus* Norman & Stebbing, 1886**

***Apseudes setiferus* Bacescu, 1981**

Genus *Atlantapseudes* Bacescu, 1978

***Atlantapseudes nigrichela* Bacescu, 1978**

Subfamily Leviapseudinae Sieg, 1983



- Genus *Fageapseudes* Bacescu & Gutu, 1971  
***Fageapseudes retusifrons*** (Richardson, 1912)
- Family Sphyrapodidae Gutu, 1980b  
 Genus *Sphyrapus* Sars, 1882  
***Sphyrapus malleolus*** Norman & Stebbing, 1886
- Suborder Tanaidomorpha Sieg, 1980**  
**Tanaidomorpha undetermined**
- Family Agathotanaidae Lang, 1971  
 Genus *Paragathotana* Lang, 1971  
***Paragathotana* sp.**  
 Genus *Paranarthrura* Hansen, 1913  
***Paranarthrura* sp.**
- Family Akanthophoreidae Sieg, 1986  
 Genus *Chaulioleona* Dojiri & Sieg, 1997  
**aff. *Chaulioleona* sp.**
- Family Colletteidae Larsen & Wilson, 2002  
 Genus *Collettea* Lang, 1973  
***Collettea* sp.**  
 Genus *Haplocope* Sars, 1882  
***Haplocope diapira*** Blazewicz-paszkwycz, Bamber & Cunha, 2011  
 Genus *Leptognathiella* Hansen, 1913  
**cf. *Leptognathiella* sp.**  
 Genus *Caudalonga* Larsen, 2005  
***Caudalonga* aff. *quatroleon*** Larsen, 2005
- Family Leptocheliidae Lang, 1973  
 Genus *Mesotana* Dollfus, 1897  
***Mesotana* pinguiculus** Blazewicz-paszkwycz, Bamber & Cunha, 2011
- Family Leptognathiidae Lang, 1976  
 Genus *Leptognathia* Sars, 1882  
***Leptognathia* cf. *gyrae*** Larsen, 2005  
***Leptognathia* spp.**
- Family Paratanaoidea incertae sedis  
 Genus *Cristatotana* Kudinova-Pasternak, 1990  
***Cristatotana* contoura** Blazewicz-paszkwycz, Bamber & Cunha, 2011
- Family Pseudotanaidae Sieg, 1976  
 Genus *Pseudotana* Sars, 1882  
***Pseudotana* tympanobaculum** Blazewicz-paszkwycz, Bamber & Cunha, 2011
- Family Typhlotanidae Sieg, 1986  
**cf. Typhlotanidae undetermined**  
 Genus *Meromonakantha* Sieg, 1986  
**aff. *Meromonakantha* sp.**  
 Genus *Torquella* Blazewicz-Paszkwycz, 2007  
***Torquella* sp1**  
***Torquella iberica*** Blazewicz-paszkwycz, Bamber & Cunha, 2011  
 Genus *Typhlotana* Sars, 1882  
***Typhlotana* kyphosis** Blazewicz-Paszkwycz, Bamber & Cunha, 2011
- Family Tanaellidae Larsen & Wilson, 2002  
 Genus *Tanaella* Norman & Stebbing, 1886  
***Tanaella unguicillata*** Norman & Stebbing, 1886
- Order Isopoda Latreille, 1817  
**Isopoda undetermined**
- Suborder Asellota Latreille, 1802**  
 Family Desmosomatidae G. O. Sars, 1897  
**Desmosomatidae undetermined**  
 Genus *Chelator* Hessler, 1970

- Chelator* sp1**  
***Chelator* cf. *insignis*** (Hansen, 1916)  
***Chelator* cf. *verecundus*** Hessler, 1970  
 Genus *Eugerd* Meinert, 1890  
***Eugerd* "tetarta type"**  
 Genus *Eugerdella* Kussakin, 1965  
***Eugerdella* cf. *ischnomesoides*** Hessler, 1970  
***Eugerdella* *pugilator*** Hessler, 1970  
***Eugerdella* aff. *pugilator*** Hessler, 1970  
 Genus *Mirabilicoxa* Hessler, 1970  
***Mirabilicoxa* cf. *acuminata*** Hessler, 1970  
 Genus *Prochelator* Hessler, 1970  
***Prochelator* *lateralis*** (Sars G.O., 1899)  
 Family Haploniscidae Hansen, 1916  
 Genus *Antennuloniscus* Menzies, 1962  
***Antennuloniscus* aff. *dimeroceras*** (Barnard, 1920)  
 Family Ischnomesidae Hansen, 1916  
**Ischnomesidae undetermined**  
 Genus *Haplomesus* Richardson, 1908  
***Haplomesus* spp. (2 species)**  
 Family Janirellidae Menzies, 1956  
 Genus *Janirella* Bonnier, 1896  
***Janirella* spp. (2 species)**  
***Janirella* *nanseni*** Bonnier, 1896  
 Family Janiridae Sars, 1897  
 Genus *Austrofilius* Hodgson, 1910  
***Austrofilius* cf. *mediterraneus*** Castello, 2002  
 Genus *Janira* Leach, 1814  
***Janira* cf. *maculosa*** Leach, 1814  
 Family Joeropsididae Nordenstam, 1933  
 Genus *Joeropsis* Koehler, 1885  
***Joeropsis* sp.**  
 Family Munnidae Sars, 1897  
 Genus *Munna* Krøyer, 1839  
***Munna* spp. (2 species)**  
 Family Munnopsidae Lilljeborg, 1864  
 Subfamily Eurycopinae Hansen, 1916  
 Genus *Disconnectes* Wilson & Hessler, 1981  
***Disconnectes* spp. (4 species)**  
 Genus *Eurycope* Sars, 1864  
***Eurycope* sp1**  
***Eurycope* *complanata* complex** Bonnier, 1896  
 Subfamily Ilyarachninae Hansen, 1916  
**Ilyarachninae undetermined**  
 Genus *Aspidarachna* Sars, 1897  
***Aspidarachna* sp.**  
 Genus *Echinozone* G.O. Sars, 1897  
**cf. *Echinozone* sp.**  
 Genus *Ilyarachna* Sars, 1870  
***Ilyarachna* sp1**  
***Ilyarachna* cf. *longicornis*** (Sars G.O., 1864)  
 Genus *Lipomera* Tattersall, 1905  
***Lipomera* (*Paralipomera*) cf. *knorrae*** Wilson, 1989  
 Genus *Pseudarachna* G.O. Sars, 1897  
***Pseudarachna* sp.**

- Pseudarachna cf. hirsuta*** (G.O. Sars, 1864)
- Family Nannoniscidae Hansen, 1916  
 Genus *Hebefustis* Siebenaller & Hessler, 1977  
**cf. *Hebefustis* sp.**  
 Genus *Nannoniscooides* Hansen, 1916  
***Nannoniscooides* sp.**  
 Genus *Nannonisconus* Schultz, 1966  
**aff. *Nannonisconus intermedius*** (Siebenaller & Hessler, 1981)  
 Genus *Nannoniscus* G.O. Sars, 1870  
***Nannoniscus* sp.**
- Family Paramunnidae Vanhöffen, 1914  
 Genus *Notoxenoides* Menzies, 1962  
***Notoxenoides* sp.**  
 Genus *Paramunna* G.O. Sars, 1866  
***Paramunna bilobata*** G.O. Sars, 1866  
 Genus *Pleurogonium* G.O. Sars, 1864  
**cf. *Pleurogonium* sp.**  
 Genus *Tethygonium* Just & Wilson, 2007  
***Tethygonium cf. variable*** (Schiecke & Modigh-Tota, 1976)
- Family Thambematidae Stebbing, 1913  
 Genus *Thambema* Stebbing, 1912  
***Thambema* sp.**
- Suborder Cymothoidea Wägele, 1989**
- Superfamily Anthuroidea Leach, 1914**
- Anthuroidea undetermined**
- Family Antheluridae Poore & Lew Ton, 1988  
 Genus *Ananthura* Barnard, 1925  
**cf. *Ananthura* sp.**
- Family Anthuridae Leach, 1814  
**Anthuridae undetermined**
- Family Hyssuridae Wägele, 1981  
**Hyssuridae undetermined**  
 Genus *Hyssura* Norman & Stebbing, 1886  
***Hyssura* spp. (2 species)**  
 Genus *Neohyssura* Amar, 1953  
***Neohyssura* sp.**
- Family Leptanthuridae Poore, 2001  
**Leptanthuridae spp. (2 species)**  
 Genus *Bulloanthura* Poore, 1978  
***Bulloanthura cf. aquitanica*** Kensley, 1982  
 Genus *Leptanthura* Sars, 1897  
***Leptanthura cf. affinis*** (Bonnier, 1896)
- Superfamily Cymothooidea Leach, 1814**
- Family Cirolanidae Dana, 1852  
 Genus *Metacirolana* Kussakin, 1979  
***Metacirolana hanseni*** (Bonnier, 1896)  
 Genus *Natatolana* Bruce, 1981  
***Natatolana borealis*** (Lilljeborg, 1851)  
***Natatolana caeca*** (Dollfus, 1903)
- Family Gnathiidae Leach, 1814  
**Gnathiidae sp1**  
 Genus *Monodgnathia* Cohen & Poore, 1994  
***Monodgnathia cristatipes*** (Stebbing, 1912)
- Order Amphipoda Latreille, 1816  
**Amphipoda undetermined**

**Suborder Gammaridea Latreille, 1802**

Family Ampeliscidae Krøyer, 1842

Genus *Ampelisca* Krøyer, 1842***Ampelisca cf. anophthalma*** Bellan-Santini & Kaim-Malka, 1977***Ampelisca dalmatina*** Karaman, 1975***Ampelisca gibba*** Sars, 1883***Ampelisca aff. typica*** (Bate, 1856)Genus *Byblis* Boeck, 1871***Byblis guernei*** Chevreux, 1887Genus *Haploops* Liljeborg, 1856***Haploops proxima*** Chevreux, 1919

Family Amphiloichidae Boeck, 1871

**cf. Amphiloichidae undetermined**Genus *Amphilochoides* Sars, 1895***Amphilochoides serratipes*** (Norman, 1869)Genus *Amphiloichus* Bate, 1862***Amphiloichus cf. brunneus*** Della Valle, 1893***Amphiloichus manudens*** Bate, 1862Genus *Gitana* Boeck, 1871**cf. *Gitana* sp.*****Gitana abyssicola*** Sars, 1895

Family Argissidae Walker, 1904

Genus *Argissa* Boeck, 1871***Argissa cf. hamatipes*** (Norman, 1869)

Family Atylidae Lilljeborg, 1865

**cf. Atylidae undetermined**Genus *Atylus* Leach, 1815***Atylus vedlomensis*** (Bate & Westwood, 1862)

Family Cressidae Stebbing, 1899

Genus *Cressa* Boeck, 1857***Cressa cristata*** Myers, 1969***Cressa cf. mediterranea*** Ruffo, 1979

Family Leucothoidae Dana, 1852

Genus *Leucothoe* Leach, 1814***Leucothoe lilljeborgi*** Boeck, 1861

Family Liljeborgiidae Stebbing, 1899

Genus *Idunella* G.O. Sars, 1894***Idunella cf. nana*** (Schecke, 1973)***Idunella pirata*** Krapp-Schickel, 1975Genus *Liljeborgia* Bate, 1862***Liljeborgia* sp.**

Family Melphidippidae Stebbing, 1899

Genus *Melphidippella* Sars, 1894***Melphidippella macra*** (Norman, 1869)

Family Oedicerotidae Lilljeborg, 1865

**Oedicerotidae undetermined**Genus *Bathymedon* Sars, 1892***Bathymedon acutifrons*** Bonnier, 1896***Bathymedon monoculodiformis*** Ledoyer, 1983Genus *Deflexilodes* Bousfield & Chevrier, 1996***Deflexilodes acutipes*** (Ledoyer, 1983)***Deflexilodes griseus*** (Della Valle, 1893)Genus *Monoculodes* Stimpson, 1853***Monoculodes packardi*** Boeck, 1871Genus *Oediceroides* Stebbing, 1888

- Oediceroides pilosa*** Ledoyer, 1983  
Genus *Periocolodes* Sars, 1895  
    ***Periocolodes longimanus*** (Bate & Westwood, 1868)  
Genus *Synchelidium* Sars, 1895  
    ***Synchelidium haplocheles*** (Grube, 1864)  
    ***Synchelidium longidigitatum*** Ruffo, 1947  
Genus *Westwoodilla* Bate, 1862  
    ***Westwoodilla caecula*** (Bate, 1857)  
Family Pardaliscidae Boeck, 1871  
    **Pardaliscidae undetermined**  
Genus *Halice* Boeck, 1871  
    ***Halice abyss*** Boeck, 1871  
    ***Halice walkeri*** (Ledoyer, 1973)  
Genus *Nicippe* Bruzelius, 1859  
    ***Nicippe tumida*** Bruzelius, 1859  
Genus *Pardaliscella* Sars, 1893  
    ***Pardaliscella cf. boeckii*** (Malm, 1870)  
Family Phoxocephalidae Sars, 1891  
    Subfamily Harpiniinae Barnard & Drummond, 1978  
    Genus *Harpinia* Boeck, 1876  
        ***Harpinia* spp. (several species)**  
        ***Harpinia cf. agna*** Karaman, 1987  
        ***Harpinia aff. ala*** Karaman, 1987  
        ***Harpinia cf. antennaria*** Meinert, 1890  
        ***Harpinia crenulata*** (Boeck, 1871)  
        ***Harpinia dellavallei*** Chevreux, 1910  
        ***Harpinia cf. pectinata*** Sars, 1891  
        ***Harpinia serrata*** G.O. Sars, 1879  
        ***Harpinia cf. truncata*** Sars, 1891  
    Subfamily Phoxocephalinae G.O. Sars, 1891  
    Genus *Leptophoxus* G. O. Sars, 1895  
        ***Leptophoxus falcatus*** (Sars, 1882)  
Genus *Metaphoxus* Bonnier, 1896  
    ***Metaphoxus simplex*** (Bate, 1857)  
Family Pleustidae Buchholz, 1874  
    **cf. Pleustidae undetermined**  
Genus *Stenopleustes* Sars, 1895  
    **cf. *Stenopleustes* sp.**  
    ***Stenopleustes latipes*** (Sars, 1858)  
Family Sebiidae Walker, 1908  
Genus *Seba* Bate, 1862  
    ***Seba aloe*** Karaman, 1971  
Family Stegocephalidae Dana, 1855  
    ***Stegocephalidae* sp.**  
Genus *Andaniexis* Stebbing, 1906  
    ***Andaniexis cf. abyss*** (Boeck, 1871) / ***A. gracilis*** Berge & Vader, 1997  
    ***Andaniexis cf. mimonectes*** Ruffo, 1975  
Genus *Phippsiella* Schellenberg, 1925  
    ***Phippsiella pseudophippsia*** Bellan-Santini, 1985  
Genus *Stegocephaloides* Sars, 1895  
    ***Stegocephaloides cf. christianiensis*** Boeck, 1871  
Family Stenothoidae Boeck, 1871  
    **Stenothoidae undetermined**  
    **Stenothoidae sp1**  
Genus *Stenothoe* Dana, 1852

*Stenothoe* aff. *eduardi* Krapp-Schickel, 1975

*Stenothoe* cf. *marina* (Bate, 1856) / *S. eduardi* Krapp-Schickel, 1975

Family Synopiidae Dana, 1853

Genus *Pseudotiron* Chevreux, 1895

*Pseudotiron bouvieri* Chevreux, 1895

Genus *Syrrhoe* Goës, 1866

*Syrrhoe affinis* Chevreux, 1908

Family Urothoidae Bousfield, 1978

Genus *Carangolia* J.L. Barnard, 1961

*Carangolia barnardi* Jaume & Sorbe, 2001

**Superfamily Eusiroidea Bousfield, 1979**

Family Eusiridae Stebbing, 1888

Genus *Eusirus* Krøyer, 1845

*Eusirus longipes* Boeck, 1861

Genus *Rhachotropis* S.I. Smith, 1883

*Rhachotropis glabra* Ledoyer, 1977

*Rhachotropis* cf. *inermis* Ledoyer, 1977

**Superfamily Lysianassoidea Dana, 1849**

Family Aristiidae Lowry & Stoddart, 1997

Genus *Aristias* Boeck, 1871

*Aristias* cf. *neglectus* Hansen, 1888

Genus *Perrierella* Chevreux & Bouvier, 1892

*Perrierella audouiniana* (Bate, 1857)

Family Lysianassidae Dana, 1849

**Lysianassidae undetermined**

Subfamily Lysianassinae Dana, 1849

Genus *Lysianassa* Milne-Edwards, 1830

*Lysianassa plumosa* Boeck, 1871

Subfamily Tryphosinae Lowry & Stoddart, 1997

Genus *Hippomedon* Boeck, 1871

cf. *Hippomedon* sp.

*Hippomedon bidentatus* Chevreux, 1903

*Hippomedon oculatus* Chevreux & Fage, 1925

Genus *Lepidepecreum* Bate & Westwood, 1868

*Lepidepecreum subclypeatum* Ruffo & Schiecke, 1977

Genus *Paracentromedon* Chevreux & Fage, 1925

*Paracentromedon crenulatus* (Chevreux, 1900)

Genus *Tryphosella* Bonnier, 1893

*Tryphosella longidactyla* Ruffo, 1985

Family Opisidae Lowry & Stoddart, 1995

Genus *Normanion* Bonnier, 1893

*Normanion ruffoi* Diviacco & Vader, 1988 / *N. chevreuxi* Diviacco & Vader, 1988

**Suborder Senticaudata Lowry & Myers, 2013**

**Infraorder Carangoliopsida Bousfield, 1977**

Family Carangoliopsidae Bousfield, 1977

Genus *Carangoliopsis* Ledoyer, 1970

*Carangoliopsis spinulosa* Ledoyer, 1970

**Infraorder Corophiida Leach, 1814 (sensu Lowry & Myers, 2013)**

**Superfamily Aoroidea Stebbing, 1899**

Family Aoridae Stebbing, 1899

**Aoridae undetermined**

Genus *Autonoe* Bruzelius, 1859

*Autonoe karamani* (Myers, 1976)

Genus *Lembos* Bate, 1857

cf. *Lembos* sp.

**Lembos spp.**Genus *Microdeutopus* Costa, 1853**Microdeutopus sp.**

Family Unciolidae Myers &amp; Lowry, 2003

Genus *Unciolella* Chevreux, 1911**cf. Unciolella sp.****Superfamily Caprelloidea Leach, 1814**

Family Caprellidae Leach, 1814

Subfamily Caprellinae Leach, 1814

Genus *Caprella* Lamarck, 1801**Caprella sp.**Genus *Liropus* Mayer, 1890**Liropus elongatus** Mayer, 1890Genus *Pseudoprotella* Mayer, 1890**Pseudoprotella phasma** Montagu, 1804

Subfamily Phtisicinae Vassilenko, 1968

Genus *Phtisica* Slabber, 1769**Phtisica marina** Slabber, 1769

Family Dulichiidae Laubitz, 1983

Genus *Dulichiosis* Laubitz, 1977**Dulichiosis nordlandica** (Boeck, 1870)

Family Podoceridae Leach, 1814

Genus *Laetmatophilus* Bruzelius, 1859**Laetmatophilus ledoyeri** Ruffo, 1986**Superfamily Photoidea Boeck, 1871**

Family Ischyroceridae Stebbing, 1899

**Ischyroceridae undetermined****Ischyroceridae sp1**Genus *Notopoma* Lowry & Berents, 1996**Notopoma sp1**

Family Photidae Boeck, 1871

**cf. Photidae undetermined**Genus *Gammaropsis* Liljeborg, 1855**Gammaropsis spp. (several species)****Gammaropsis cf. crenulata** Krapp-Schickel & Myers, 1979Genus *Megamphopus* Norman, 1869**Megamphopus cf. brevidactylus** Myers, 1976Genus *Photis* Krøyer, 1842**cf. Photis sp.****Photis longicaudata** (Bate & Westwood, 1862)**Infraorder Hadziida S. Karaman, 1943**

Family Eriopisidae Lowry &amp; Myers, 2013

Genus *Eriopisa* Stebbing, 1890**Eriopisa elongata** (Bruzelius, 1859)

Family Maeridae Krapp-Schickel, 2008

Genus *Maera* Leach, 1814**Maera spp.****Maera aff. loveni** (Bruzelius, 1859)Genus *Othomaera* Krapp-Schickel, 2000**Othomaera othonis** (Milne-Edwards, 1830)**Class Maxillopoda** Dahl, 1956**Subclass Thecostraca** Gruvel, 1905**Infraclass Cirripedia** Burmeister, 1834

Superorder Thoracica Darwin, 1854

Order Sessilia Lamarck, 1818

Family Verrucidae Darwin, 1854  
 Genus *Verruca* Schumacher, 1817

***Verruca* sp1**

Order Scalpelliformes Buckeridge & Newman, 2006  
**Scalpelliformes undetermined**

**Subphylum Chelicerata**

**Class Pycnogonida** Latreille, 1810  
**Pycnogonida spp. (2 species)**

**Phylum MOLLUSCA**

**Class Solenogastres** Gegenbaur, 1878  
**Solenogastres undetermined**

**Class Caudofoveata** C. R. Boettger, 1956

Order Chaetodermatida Simroth, 1893  
 Family Chaetodermatidae Théel, 1875  
**Chaetodermatidae undetermined**

**Class Gastropoda** Cuvier, 1795

**Subclass Caenogastropoda Cox, 1960**

Family Cerithiidae Fleming, 1822

***Cerithiidae* sp1**

Family Eulimidae Philippi, 1853

Genus *Melanella* Bowdich, 1822

***Melanella* sp1**

Family Nystiellidae Clench & Turner, 1952

Genus *Iphitus* Jeffreys, 1883

***Iphitus marshalli* (Sykes, 1925)**

Order Littorinimorpha Golikov & Starobogatov, 1975

Family Rissoidae Gray, 1847

Genus *Alvania* Risso, 1826

***Alvania cimicoides* (Forbes, 1844)**

***Alvania porcupinae* Gofas & Warén, 1982**

Genus *Pseudosetia* Monterosato, 1884

**cf. *Pseudosetia* sp.**

Order Neogastropoda Wenz, 1938

Family Buccinidae Rafinesque, 1815

Genus *Chauvetia* Monterosato, 1884

***Chauvetia balgimae* Gofas & Oliver, 2010**

Family Columbelloidea Swainson, 1840

Genus *Amphissa* H. Adams & A. Adams, 1853

***Amphissa acutecostata* (Philippi, 1844)**

Family Marginellidae Fleming, 1828

**Marginellidae sp1**

**Subclass Heterobranchia**

Family Pyramidellidae Gray, 1840

Genus *Turbonilla* Risso, 1826

***Turbonilla* sp1**

Order Nudibranchia Cuvier, 1817

**Nudibranchia undetermined**

Order Pleurobranchomorpha

**cf. Pleurobranchomorpha undetermined**

**Subclass Vetigastropoda Salvini-Plawen, 1980**

Family Lepetelloidea Dall, 1882

Genus *Lepetella* Verrill, 1880

***Lepetella* sp1**

**Class Bivalvia** Linnaeus, 1758

**Bivalvia undetermined**



**Subclass Protobranchia Pelseneer, 1889**

- Order Nuculanoida Carter, D.C. Campbell & M.R. Campbell, 2000  
 Family Neilonellidae Schileyko, 1989  
 Genus *Neilonella* Dall, 1881  
     *Neilonella latior* (Jeffreys, 1876)  
 Family Nuculanidae H. Adams & A. Adams, 1858 (1854)  
 Genus *Ledella* Verrill & Bush, 1897  
     *Ledella messanensis* (Jeffreys, 1870)  
 Genus *Saccella* Woodring, 1925  
     *Saccella commutata* (Philippi, 1844)  
 Family Yoldiidae Dall, 1908  
 Genus *Microgloma* Sanders & Allen, 1973  
     *Microgloma sp1*  
     *Microgloma pusilla* (Jeffreys, 1879)  
     *Microgloma tumidula* (Monterosato, 1880)
- Order Nuculida Dall, 1889  
 Family Nuculidae Gray, 1824  
 Genus *Ennucula* Iredale, 1931  
     *Ennucula aegeensis* (Forbes, 1844)  
     *Ennucula corbuloides* (Seguenza, 1877)
- Order Solemyoida Dall, 1889  
 Family Solemyidae Gray, 1840  
 Genus *Solemya* Lamarck, 1818  
     *Solemya elarraichensis* Oliver, Rodrigues & Cunha, 2011

**Subclass Pteriomorphia Beurlen, 1944**

- Order Arcoidea Stoliczka, 1871  
 Family Arcidae Lamarck, 1809  
 Genus *Bathyarca* Kobelt, 1891  
     *Bathyarca philippiana* (Nyst, 1848)
- Family Limopsidae Dall, 1895  
 Genus *Limopsis* Sassi, 1827  
     *Limopsis minuta* (Philippi, 1836)
- Order Limoida Moore, 1952  
 Family Limidae Rafinesque, 1815  
 Genus *Limatula* S. V. Wood, 1839  
     *Limatula subovata* (Monterosato, 1875)
- Order Mytiloida Ferussac, 1822  
 Family Mytilidae Rafinesque, 1815  
     *Mytilidae sp1*  
 Genus *Dacrydium* Torell, 1859  
     *Dacrydium balgimi* Salas & Gofas, 1997
- Order Pectinoida Gray, 1854  
 Family Pectinidae Rafinesque, 1815  
 Genus *Delectopecten* Stewart, 1930  
     *Delectopecten vitreus* (Gmelin, 1791)
- Family Propeamussiidae R.T. Abbott, 1954  
 Genus *Cyclopecten* A. E. Verrill, 1897  
     *Cyclopecten hoskynsi* (Forbes, 1844)

**Subclass Heterodonta Neumayr, 1884**

- Order Veneroida Gray, 1854  
 Family Kelliellidae Fischer, 1887  
 Genus *Kelliella* M. Sars, 1870  
     *Kelliella miliaris* (Philippi, 1844)
- Family Semelidae Stoliczka, 1870 (1825)  
 Genus *Abra* Lamarck, 1818

***Abra longicallus*** (Scacchi, 1835)

Order Anomalodesmata Dall, 1889

Family Cuspidariidae Dall, 1886

Genus *Cuspidaria* Nardo, 1840

***Cuspidaria* sp1**

Genus *Tropidomya* Dall & Smith, 1886

***Tropidomya abbreviata*** (Forbes, 1843)

Order Lucinoidea Gray, 1854

Family Thyasiridae Dall, 1900 (1895)

**Thyasiridae undetermined**

Genus *Leptaxinus* Verrill & Bush, 1898

***Leptaxinus minutus*** Verrill & Bush, 1898

Class Scaphopoda Bronn, 1862

**Scaphopoda spp. (6 species)**

Phylum BRYOZOA

**Bryozoa undetermined**

Phylum BRACHIOPODA Duméril, 1806

**Brachiopoda undetermined**

Phylum ECHINODERMATA Bruguère, 1791

Subphylum Crinozoa

Class Crinoidea

**Crinoidea undetermined**

Subphylum Asterozoa

Class Ophiuroidea Gray, 1840

**Ophiuroidea undetermined**

Order Ophiurida Müller & Troschel, 1840

Family Amphiuridae Ljungman, 1867

**Amphiuridae undetermined**

Genus *Amphipholis* Ljungman, 1866

***Amphipholis squamata*** (Delle Chiaje, 1828)

Genus *Amphiura* Forbes, 1843

***Amphiura* sp1**

***Amphiura chiajei*** Forbes, 1843

***Amphiura filiformis*** (O.F. Müller, 1776)

***Amphiura grandisquama*** Lyman, 1869

Family Ophiacanthidae Ljungman, 1867

**Ophiacanthidae undetermined**

Genus *Ophiacantha* Müller & Troschel, 1842

***Ophiacantha abyssicola*** G.O. Sars, 1871

***Ophiacantha bidentata*** (Bruzellius, 1805)

Genus *Ophiactis* Lütken, 1856

***Ophiactis cf. balli*** (W. Thompson, 1840)

Subphylum Echinozoa

Class Echinoidea Leske, 1778

Order Spatangoida L. Agassiz, 1840

Family Brissidae Gray, 1855

Genus *Brissopsis* L. Agassiz, 1840

***Brissopsis lyrifera*** (Forbes, 1841)

Class Holothuroidea

**Holothuroidea Undetermined**

Phylum Chordata

Class Ascidiacea Nielsen, 1995

Order Phlebobranchia Lahille, 1886

Family Ascidiidae Herdman, 1882

**Ascidiidae undetermined**

**MEIOFAUNA****Phylum NEMATODA****Nematoda undetermined****Phylum ARTHROPODA****Subphylum Crustacea****Class Maxillopoda** Dahl, 1956

Subclass Copepoda

**Copepoda undetermined**

Subclass Ostracoda Latreille, 1802

**Ostracoda undetermined****Class Arachnida Cuvier, 1812**

Order Trombidiformes

Family Halacaridae Murray, 1877

**Halacaridae undetermined****This list was compiled in collaboration with several specialists:**

**Almeida, Mariana D.\*** (Arthropoda: Mysida); **Cunha, Marina R.\*** (Arthropoda); **Génio, Luciana\*** (Mollusca: Gastropoda); **Moura, Carlos J.\*\*** (Cnidaria: Hydrozoa); **Ravara, Ascensão \*** (Polychaeta); **Rodrigues, Clara F.\*** (Mollusca: Bivalvia; Echinodermata; among other taxa)

\* Departamento de Biologia (Dbio) and Centro de Estudos do Ambiente e do Mar (CESAM), Universidade de Aveiro

\*\* Departamento de Oceanografia e Pescas, Universidade dos Açores

**References for cryptic species:**

Moura, C.J., 2011. Systematics and evolution of coastal and deep-water Hydrozoa from the NE Atlantic. PhD in Biology, Universidade de Aveiro, 304 pp.

Moura C.J.; Cunha M.R.; Porteiro F.M.; Rogers A.D., 2011. Polyphyly and cryptic diversity in the hydrozoan families Lafoeidae and Hebellidae (Cnidaria: Hydrozoa). *Invertebrate Systematics*, **25(5)**: 454-470.

Moura C.J.; Cunha M.R.; Porteiro F.M.; Yesson C.; Rogers A.D., 2012. Evolution of *Nemertesia* hydroids (Cnidaria: Hydrozoa, Plumulariidae) from the shallow and deep waters of the NE Atlantic and W Mediterranean. *Zoologica Scripta*, **41(1)**: 79-96.

## Annex IV

**Table I.** Breakdown of percentage contributions from SIMPER analysis for comparisons between “Geological Features” (Quantitative data). The taxa listed contribute at least 2%. Numbers in **bold** mark the 6 dominant species in each site.

Taxa	Total:	Density (ind.10dm <sup>2</sup> )				TG	LF	Contribution (%)									
		MV	PDE	M	OM			MV	PDE	M	OM	MV/PDE	MV/M	MV/OM	PDE/M	PDE/OM	M/OM
		AS:	AS:	AS:	AS:			AD:	AD:	AD:	AD:	AD:	AD:	AD:	AD:	AD:	AD:
<b>Sipuncula</b>		104.08	34.45	120.41	35.25			15.4	18.9	24.2	19.6	88.3	84.0	88.2	85.2	82.1	84.1
Sipuncula und.		2.24	<b>3.92</b>	<b>7.42</b>	<b>2.23</b>	SR-Dt	D-F	9.38	26.01	15.06	7.67	2.80	2.36	2.61	2.92	4.85	3.28
<b>Annelida</b>																	
Scolecida	cf. <i>Notomastus</i> sp.	1.02	0.57	2.04	0.74	SS-De	D-F	•	•	4.50	2.51	•	•	•	•	2.23	•
	Maldanidae und.	1.63	0.57	<b>5.19</b>	0.37	SS-De	D-T	4.13	•	5.01	•	•	•	•	2.58	•	2.47
	<i>Ophelina abranchiata</i>	0.20	0.82	1.48	1.11	SS-De	M-F	-	•	3.50	7.22	•	•	•	•	2.84	•
	<i>Aricidea</i> sp1	0.41	0.57	1.86	0.56	SR-De	D-B	-	•	•	2.26	•	•	•	•	•	•
	<i>Levinsenia</i> spp.	<b>2.86</b>	<b>1.22</b>	<b>3.15</b>	<b>1.67</b>	SR-De	D-B	2.34	6.18	5.89	4.03	•	•	2.03	2.46	3.17	2.62
	<i>Paradoneis</i> spp.	<b>4.90</b>	0.73	1.30	0.74	SR-De	D-B	4.75	2.76	3.40	3.61	2.54	2.05	2.61	•	2.22	•
Canalipalpata	<i>Siboglinum</i> spp.	<b>14.08</b>	<b>1.31</b>	<b>9.09</b>	-	SR-Ch	S-T	15.63	•	•	-	5.02	3.62	4.87	2.09	•	•
	<i>Laubieriopsis cabiochi</i>	1.02	0.33	0.19	0.56	SR-De	D-B	-	•	-	2.19	•	•	•	•	•	•
	Ampharetidae sp1	0.61	-	2.97	<b>2.04</b>	SR-De	D-T	•	-	3.02	-	•	•	•	•	•	2.13
	<i>Spiochaetopterus bergensis/typicus</i>	0.41	<b>1.06</b>	<b>3.15</b>	0.19	SR-Su	S-T	-	2.85	3.11	-	•	•	•	2.31	2.00	2.11
	<i>Prionospio</i> spp.	2.04	-	<b>3.90</b>	-	SR-De	D-T	•	-	4.40	-	•	•	•	2.13	-	2.11
	<i>Spiophanes</i> sp.	-	-	2.04	-	SR-De	D-T	-	-	2.54	-	-	•	-	•	-	•
Errantia	Exogoninae und.	0.41	0.08	2.60	-	SR-He-mic	M-F	•	-	4.74	-	•	•	•	2.17	•	2.14
	<i>Glycera lapidum</i>	1.63	0.65	2.04	<b>1.67</b>	SS-Pr-mac	M-F	5.03	•	5.99	10.07	•	•	2.04	2.13	3.22	•
	<i>Phyllodoce madeirensis</i>	0.61	-	0.74	-	SS-Sc-mac	M-F	2.09	-	•	-	•	•	•	•	-	•
	<i>Chloenopsis atlantica</i>	0.82	-	2.60	-	SS-Pr-mac	M-F	2.50	-	•	-	•	•	•	•	-	•
	<i>Paradiopatra</i> cf. <i>hispanica</i>	<b>3.88</b>	<b>3.51</b>	2.97	<b>4.82</b>	SR-Om-mac	D-T	7.12	21.49	4.39	28.76	3.49	2.13	3.59	2.40	4.93	2.62

Table I. Continued.

Taxa	Density (ind.10dm <sup>2</sup> )					Contribution (%)											
	MV	PDE	M	OM	TG	LF	MV	PDE	M	OM	MV/PDE	MV/M	MV/OM	PDE/M	PDE/OM	M/OM	
	AS:	AS:	AS:	AS:			AD:	AD:	AD:	AD:	AD:	AD:					
<b>Total:</b>	104.08	34.45	120.41	35.25			15.4	18.9	24.2	19.6	88.3	84.0	88.2	85.2	82.1	84.1	
<b>Annelida</b>																	
Oligochaeta	Oligochaeta und.	3.47	0.16	1.11	0.37	SS-Om-mic	M-F	3.1	•	•	•	•	•	•	•	•	•
<b>Arthropoda</b>																	
Leptostraca	Nebaliacea sp.	11.02	-	-	-	SR-Sc-mac	M-F	-	-	-	-	•	•	•	-	-	-
Tanaidacea	<i>Atlantapseudes nigrichela</i>	0.20	3.10	1.86	1.86	SR-Dt	D-F	-	15.03	•	8.16	2.48	•	•	2.20	4.15	•
	<i>Sphyrapus malleolus</i>	0.41	0.24	2.04	0.74	SR-Dt	D-F	•	•	•	4.30	•	•	•	•	2.05	•
Isopoda	<i>Chelator cf. verecundus</i>	0.20	0.98	1.86	0.37	SS-Om-mic	M-F	-	2.18	•	•	•	•	•	•	•	•
Amphipoda	<i>Harpinia</i> spB	0.20	-	1.11	0.93	SR-Pr-mei	M-B	-	-	•	2.35	•	•	•	•	•	•
	<i>Harpinia</i> spC	1.63	0.98	0.74	0.19	SR-Pr-mei	M-B	3.92	4.22	-	-	•	•	•	•	•	•
	<i>Harpinia</i> spD	-	0.16	-	0.93	SR-Pr-mei	M-B	-	-	-	2.15	•	-	•	•	•	•
	<i>Stenothoe cf. marina/eduardi</i>	2.86	0.33	0.37	-	SR-Pr-mac	M-F	5.85	•	•	-	2.30	•	2.16	•	•	•
	<i>Liropus elongatus</i>	1.43	-	1.30	-	SR-He-mic	M-F	2.94	-	•	-	•	•	•	•	-	•
<b>Mollusca</b>																	
Bivalvia	<i>Ennucula aegeensis</i>	0.20	0.16	-	0.74	SS-De	M-F	-	•	-	3.31	•	•	•	•	•	•
	<i>Abra longicallus</i>	1.02	0.49	2.04	0.74	SR-De	D-F	2.33	•	•	3.94	•	•	•	•	2.07	•
<b>Echinodermata</b>																	
Ophiuroidea	<i>Amphipholis squamata</i>	1.43	0.49	-	-	SR-Su	D-F	2.13	•	-	-	•	•	•	•	•	-
Echinoidea	<i>Brissopsis lyrifera</i>	-	0.33	1.11	0.19	SS-De	D-B	-	•	2.49	-	•	•	•	•	•	•
% Contribution of selected taxa:		60.39	66.11	56.70	67.37												

MV: mud volcano; PDE: Pen Duick Escarpment; M: mound; OM: off mound; TG: trophic guild; LF: life style; AS: average similarity; AD: average dissimilarity; SR: surface; SS: subsurface; He: herbivorous; Om: omnivorous; mic: microfauna; mei: meiofauna; mac: macrofauna; De: deposit feeder; Dt: detritus feeder; Su: suspension feeder; Pr: predator; Sc: scavenger; Ch: chemosynthetic; M: motile; D: discretely motile; S: sessile; F: free living; T: tubicolous; B: burrow-dwelling; •: contributions lower than 2%; -: null contributions.

**Table II.** Breakdown of percentage contributions from SIMPER analysis for comparisons between “Presence of Hard Substrates” (Quantitative data). The taxa listed contribute at least 2%. Numbers in **bold** mark the 6 dominant species in each site.

Taxa	Density (ind.10dm <sup>2</sup> )						Contribution (%)					
	Total:	C	CD	A	TG	LF	C	CD	A	C/CD	C/A	CD/A
		AS:	AS:	AS:			AD:	AD:	AD:			
	Total:	66.29	37.59	27.99			17.4	23.4	12.3	80.5	86.5	83.2
<b>Sipuncula</b>												
	Sipuncula und.	<b>5.55</b>	<b>2.72</b>	<b>1.17</b>	SR-Dt	D-F	27.57	13.52	2.79	4.17	5.10	4.16
<b>Annelida</b>												
Scolecida	cf. <i>Notomastus</i> sp.	1.39	0.68	-	SS-De	D-F	5.14	•	-	2.31	2.02	•
	Maldanidae und.	<b>2.37</b>	1.19	0.29	SS-De	D-T	2.07	•	-	2.05	1.65	•
	<i>Ophelina abbranchiata</i>	0.73	<b>1.36</b>	<b>0.87</b>	SS-De	M-F	•	3.78	9.42	2.55	2.14	3.10
	<i>Levinsenia</i> spp.	1.71	<b>1.53</b>	<b>2.33</b>	SR-De	D-B	4.08	7.17	12.27	2.82	3.47	3.95
	<i>Paradoneis</i> spp.	0.73	1.02	<b>1.17</b>	SR-De	D-B	2.95	•	17.36	•	2.31	2.84
Canalipalpata	<i>Siboglinum</i> spp.	<b>4.90</b>	0.85	-	SR-Ch	S-T	2.40	-	-	2.13	1.66	•
	Ampharetidae sp1	<b>2.20</b>	-	-	SR-De	D-T	•	-	-	•	•	-
	<i>Spiochaetopterus bergensis/typicus</i>	1.39	0.17	0.87	SR-Su	S-T	2.17	-	4.83	•	2.64	2.23
Errantia	<i>Glycera lapidum</i>	1.47	1.02	0.58	SS-Pr-mac	M-F	4.28	2.05	2.95	2.44	2.31	2.24
	cf. <i>Lumbrineris</i> sp1	0.16	-	0.58	SS-Pr-mei	M-F	-	-	2.73	•	1.23	•
	<i>Paradiopatra</i> cf. <i>hispanica</i>	<b>3.84</b>	<b>3.91</b>	<b>3.79</b>	SR-Om-mac	D-T	15.57	26.12	25.47	3.95	4.64	4.96
<b>Arthropoda</b>												
Tanaidacea	<i>Atlantapseudes nigrichela</i>	<b>2.86</b>	<b>2.72</b>	<b>1.46</b>	SR-Dt	D-F	8.21	17.86	4.30	3.83	3.55	4.37
	<i>Fageapseudes retusifrons</i>	0.73	<b>1.36</b>	-	SR-Dt	D-F	•	•	-	•	•	•
	<i>Sphyrapus malleolus</i>	0.98	0.51	0.58	SR-Dt	D-F	•	•	3.70	•	1.83	•

Table II. Continued.

Taxa		Density (ind.10dm <sup>2</sup> )			TG	M&H	Contribution (%)					
		C	CD	A			C	CD	A	C/CD	C/A	CD/A
		AS:	AS:	AS:			AD:	AD:	AD:	AD:	AD:	AD:
Total:		66.29	37.59	27.99			17.4	23.4	12.3	80.5	86.5	83.2
<b>Arthropoda</b>												
Isopoda	<i>Chelator cf. verecundus</i>	1.31	0.68	0.29	SS-Om-mic	M-F	2.22	•	-	•	1.59	•
	<i>Eugerda "tetarta type"</i>	0.57	0.17	0.87	SS-Om-mic	M-F	•	-	2.79	•	1.61	•
Amphipoda	<i>Harpinia</i> spB	0.33	0.34	0.87	SR-Pr-mei	M-B	-	-	2.94	•	1.46	•
	<i>Harpinia</i> spC	0.90	1.02	-	SR-Pr-mei	M-B	2.16	2.48	-	•	1.19	•
	<i>Paracentromedon crenulatus</i>	0.16	-	0.58	SR-Sc-mac	M-F	•	-	3.30	•	1.43	•
<b>Mollusca</b>												
Bivalvia	<i>Ennucula aegeensis</i>	0.24	0.17	0.58	SS-De	M-F	•	-	2.29	•	1.27	•
	<i>Ennucula corbuloides</i>	0.08	1.19	-	SS-De	M-F	•	8.57	-	2.36	0.28	2.74
	<i>Abra longicallus</i>	0.82	1.02	0.58	SR-De	D-F	•	3.00	2.87	2.08	1.62	2.44
% Contribution of selected taxa:		53.45	62.90	62.50								

C: presence of coral or carbonate concretions at sediment surface; CD: presence of coral or carbonate concretions at sediment subsurface; A: absence of coral or carbonate concretions on sediment; TG: trophic guild; LF: life style; AS: average similarity; AD: average dissimilarity; SR: surface; SS: subsurface; Om: omnivorous; mic: microfauna; mei: meiofauna; mac: macrofauna; De: deposit feeder; Dt: detritus feeder; Su: Suspension feeder; Pr: predator; Sc: scavenger; Ch: chemosynthetic; M: motile; D: discretely motile; S: sessile; F: free living; T: tubiculous; B: burrow-dwelling; •: contributions lower than 2%; - : null contributions.

**Table III.** Breakdown of percentage contributions from SIMPER analysis for comparisons between “Depth Zones” (Quantitative data). The taxa listed contribute at least 2%. Numbers in **bold** mark the 6 dominant species in each site.

Taxa		Density (ind.10dm <sup>2</sup> )			TG	LF	Contribution (%)					
		Z1	Z2	Z3			Z1	Z2	Z3	Z1/Z2	Z1/Z3	Z2/Z3
		AS:	AS:	AS:			AD:	AD:	AD:			
	Total:	87.76	32.12	53.83			19.3	18.8	22.5	83.9	82.3	83.3
<b>Sipuncula</b>												
	Sipuncula und.	<b>4.72</b>	<b>3.19</b>	<b>6.89</b>	SR-Dt	D-F	14.01	14.06	43.42	3.67	3.30	5.43
<b>Annelida</b>												
Scolecida	cf. <i>Notomastus</i> sp.	1.40	0.71	0.77	SS-De	D-F	3.21	•	•	2.06	•	•
	Maldanidae und.	<b>4.46</b>	0.18	-	SS-De	D-T	7.16	•	-	2.76	2.53	•
	<i>Ophelina abranchiata</i>	0.64	<b>1.06</b>	<b>1.79</b>	SS-De	M-F	•	3.78	6.16	•	2.14	2.95
	<i>Levinsenia</i> spp.	<b>2.93</b>	<b>0.98</b>	1.79	SR-De	D-B	6.83	3.53	12.90	2.98	2.81	3.08
	<i>Paradoneis</i> spp.	1.02	0.71	1.02	SR-De	D-B	3.44	3.22	2.33	•	•	2.15
Canalipalpata	<i>Siboglinum</i> spp.	<b>7.53</b>	0.53	-	SR-Ch	S-T	6.15	-	-	2.88	2.56	•
	<i>Laubieriopsis cabiochi</i>	0.13	0.35	0.77	SR-De	D-B	-	•	2.23	•	•	•
	Ampharetidae sp1	<b>3.44</b>	-	-	SR-De	D-T	2.93	-	-	•	•	-
	<i>Spiochaetopterus bergensis/typicus</i>	1.91	0.44	<b>2.81</b>	SR-Su	S-T	3.65	•	2.73	2.35	2.77	2.74
	<i>Prionospio</i> spp.	1.66	-	<b>2.04</b>	SR-De	D-T	•	-	•	•	•	•
Errantia	Exogoninae und.	1.66	0.09	0.26	SR-He-mic	M-F	2.01	-	-	•	•	•
	<i>Glycera lapidum</i>	1.53	<b>1.24</b>	0.51	SS-Pr-mac	M-F	4.13	4.62	•	2.26	•	2.04
	<i>Paradiopatra cf. hispanica</i>	<b>4.97</b>	<b>3.28</b>	<b>2.30</b>	SR-Om-mac	D-T	12.47	29.33	4.46	3.81	3.56	4.27
<b>Arthropoda</b>												
Cumacea	Leuconidae spB	-	0.09	1.02	SR-He-mic	M-F	-	-	2.02	•	•	•



Table III. Continued.

Taxa		Density (ind.10dm <sup>2</sup> )			TG	M&H	Contribution (%)					
		Z1	Z2	Z3			Z1	Z2	Z3	Z1/Z2	Z1/Z3	Z2/Z3
		AS:	AS:	AS:			AD:	AD:	AD:	AD:	AD:	AD:
	Total:	87.76	32.12	53.83			19.3	18.8	22.5	83.9	82.3	83.3
<b>Arthropoda</b>												
Tanaidacea	<i>Atlantapseudes nigrichela</i>	2.55	<b>3.02</b>	1.02	SR-Dt	D-F	5.52	17.28	•	3.24	2.34	3.68
	<i>Sphyrapus malleolus</i>	1.53	0.27	0.77	SR-Dt	D-F	•	•	2.28	•	•	•
Isopoda	<i>Chelator cf. verecundus</i>	1.53	0.53	1.53	SS-Om-mic	M-F	2.13	•	•	•	•	•
	<i>Eugerda "tetarta type"</i>	0.89	0.09	1.53	SS-Om-mic	M-F	•	-	2.32	•	•	•
	<i>Pseudarachna cf. hirsuta</i>	0.13	-	<b>2.81</b>	SS-Om-mic	M-F	-	-	-	•	•	•
Amphipoda	<i>Harpinia</i> spB	0.51	0.35	0.77	SR-Pr-mei	M-B	-	•	2.18	•	•	•
<b>Mollusca</b>												
Bivalvia	<i>Abra longicallus</i>	1.40	0.53	1.02	SR-De	D-F	•	2.42	•	•	•	•
<b>Echinodermata</b>												
Echinoidea	<i>Brissopsis lyrifera</i>	0.89	0.35	-	SS-De	D-B	2.22	•	-	•	•	•
% Contribution of selected taxa:		54.07	56.08	58.29								

Z1: depth zone 1 (<540 m depth, top of the scarp); Z2: depth zone 2 (540-640 m depth, scarp); Z3: depth zone 3 (>640 m depth, base of the scarp); TG: trophic guild; LF: life style; AS: average similarity; AD: average dissimilarity; SR: surface; SS: subsurface; He: herbivorous; Om: omnivorous; mic: microfauna; mei: meiofauna; mac: macrofauna; De: deposit feeder; Dt: detritus feeder; Su: suspension feeder; Pr: predator; Ch: chemosynthetic; M: motile; D: discretely motile; S: sessile; F: free living; T: tubicolous; B: burrow-dwelling; •: contributions lower than 2%; -: null contributions.



Table IV. Continued.

Taxa	Frequency of occurrence						Contribution (%)										
	MV	PDE	M	OM	TG	M&H	MV	PDE	M	OM	MV/PDE	MV/M	MV/OM	PDE/M	PDE/OM	M/OM	
	n	13	41	26			14	AS:	AS:	AS:	AS:	AD:	AD:	AD:	AD:	AD:	AD:
<b>S</b>	219	244	258	120			22.6	18.5	20.5	19.4	85.3	81.2	85.4	84.1	82.1	85.0	
<b>Arthropoda</b>																	
Tanaidacea	<i>Atlantapseudes nigrichela</i>	0.31	<b>0.59</b>	0.42	<b>0.64</b>	SR-Dt	D-F	•	9.93	2.35	14.19	•	•	•	1.56	1.95	1.74
	<i>Sphyrapus malleolus</i>	0.31	0.29	0.35	0.29	SR-Dt	D-F	•	2.45	•	2.00	•	•	•	•	1.59	•
Amphipoda	<i>Ampelisca dalmatina</i>	<b>0.54</b>	0.07	0.23	0.07	SR-Su	D-T	2.83	•	•	-	•	•	•	•	•	•
	<i>Oediceroides pilosa</i>	0.46	0.12	0.19	-	SS-Pr-mei	M-F	2.15	•	•	-	•	•	•	•	•	•
	<i>Harpinia</i> spB	0.23	0.17	0.27	0.29	SR-Pr-mei	M-B	•	•	•	2.44	•	•	•	•	•	•
	<i>Harpinia</i> spC	0.38	0.41	0.15	0.14	SR-Pr-mei	M-B	•	3.72	•	•	•	•	•	•	1.50	•
	<i>Harpinia</i> spD	-	0.05	0.04	0.29	SR-Pr-mei	M-B	-	-	-	2.04	•	•	•	•	•	•
	<i>Liropus elongatus</i>	<b>0.62</b>	0.12	0.46	-	SR-He-mic	M-F	4.28	•	3.25	-	•	•	•	•	•	•
<b>Mollusca</b>																	
Bivalvia	<i>Ennucula aegeensis</i>	0.15	0.05	0.08	0.36	SS-De	M-F	•	-	•	3.24	•	•	•	•	•	•
	<i>Abra longicallus</i>	<b>0.54</b>	0.24	0.42	<b>0.71</b>	SR-De	D-F	3.38	•	2.59	16.98	•	•	•	•	2.51	1.77
<b>Echinodermata</b>																	
Ophiuroidea	<i>Amphipholis squamata</i>	<b>0.54</b>	0.12	0.31	-	SR-Su	D-F	3.36	•	2.04	-	•	•	•	•	•	•
% Contribution of selected taxa to the total species richness:		12.79	12.30	11.24	21.67												

MV: mud volcano; PDE: Pen Duick Escarpment; M: mound; OM: off mound; TG: trophic guild; LF: life style; AS: average similarity; AD: average dissimilarity; SR: surface; SS: subsurface; He: herbivorous; Om: omnivorous; mic: microfauna; mei: meiofauna; mac: macrofauna; De: deposit feeder; Dt: detritus feeder; Su: suspension feeder; Pr: predator; Sc: scavenger; Ch: chemosynthetic; M: motile; D: discretely motile; S: sessile; F: free living; T: tubiculous; B: burrow-dwelling; •: contributions lower than 1.5 (AD) or 2.0% (AS); -: null contributions.

**Table V.** Breakdown of percentage contributions from SIMPER analysis for comparisons between “Presence of Hard Substrates” (Qualitative data). The taxa listed contribute at least 2.0% for average similarity within groups (AS) or at least 1.5% for dissimilarity between groups (AD). Numbers in **bold** mark the most frequent species (above 0.50 of frequency of occurrence) in each site.

Taxa	Frequency of occurrence						Contribution (%)						
		C	CD	A			C	CD	A	C/CD	C/A	CD/A	
	n	41	18	14	TG	LF	AS:	AS:	AS:	AD:	AD:	AD:	
<b>Sipuncula</b>		<b>S</b>	295	166	145			17.2	21.5	13.3	80.9	85.3	82.7
	Sipuncula und.	<b>0.78</b>	<b>0.78</b>	0.36	SR-Dt	D-F	16.91	13.72	5.51	•	2.08	2.13	
<b>Annelida</b>													
	Scolecida												
	cf. <i>Notomastus</i> sp.	0.46	0.28	0.21	SS-De	D-F	4.99	•	•	1.53	1.55	•	
	Maldanidae und.	0.34	0.28	0.29	SS-De	D-T	2.38	•	2.18	•	•	•	
	<i>Ophelina abbranchiata</i>	0.24	0.33	0.43	SS-De	M-F	•	2.67	7.44	•	1.61	1.75	
	<i>Levinsenia</i> spp.	0.37	<b>0.56</b>	<b>0.50</b>	SR-De	D-B	3.78	5.44	8.88	1.66	1.77	1.82	
	<i>Paradoneis</i> spp.	0.39	0.33	<b>0.57</b>	SR-De	D-B	3.41	1.67	11.41	•	1.78	1.81	
	Canalipalpata												
	<i>Spiochaetopterus bergensis/typicus</i>	0.32	0.33	0.29	SR-Su	S-T	2.24	1.98	2.54	•	•	•	
	Errantia												
	Syllinae und.	0.34	0.22	0.21	SR-Pr-mei	M-F	2.32	•	•	•	•	•	
	<i>Glycera lapidum</i>	0.41	0.44	0.36	SS-Pr-mac	M-F	3.73	3.40	3.11	1.54	1.50	1.60	
	<i>Paradiopatra</i> cf. <i>hispanica</i>	<b>0.71</b>	<b>0.78</b>	<b>0.50</b>	SR-Om-mac	D-T	13.70	13.01	8.71	•	1.90	1.95	
<b>Arthropoda</b>													
	Cumacea												
	Leuconidae spA	0.10	0.39	0.21	SR-He-mic	M-F	•	3.02	1.56	•	•	1.56	
	Tanaidacea												
	<i>Atlantapseudes nigrichela</i>	0.46	<b>0.78</b>	0.43	SR-Dt	D-F	5.66	14.96	6.96	1.84	1.76	2.08	
	<i>Fageapseudes retusifrons</i>	0.12	0.39	0.14	SR-Dt	D-F	•	2.81	•	•	•	•	
	<i>Sphyrapus malleolus</i>	0.34	0.39	0.21	SR-Dt	D-F	3.03	2.59	•	1.50	•	•	

Table V. Continued.

Taxa	Frequency of occurrence						Contribution (%)					
		C	CD	A			C	CD	A	C/CD	C/A	CD/A
	n	41	18	14	TG	H	AS:	AS:	AS:	AD:	AD:	AD:
	S	295	166	145			17.2	21.5	13.3	80.9	85.3	82.7
<b>Arthropoda</b>												
Isopoda	<i>Eugerdia</i> "tetarta type"	0.07	0.11	0.29	SS-Om-mic	M-F	•	•	2.72	•	•	•
Amphipoda	<i>Harpinia</i> spB	0.17	0.22	0.29	SR-Pr-mei	M-B	•	•	2.36	•	•	•
	<i>Harpinia</i> spC	0.29	0.44	0.21	SR-Pr-mei	M-B	1.68	3.35	•	•	•	1.53
<b>Mollusca</b>												
Bivalvia	<i>Ennucula corbuloides</i>	0.15	0.39	0.14	SS-De	M-F	•	3.12	•	•	•	1.51
	<i>Abra longicallus</i>	0.37	<b>0.50</b>	0.29	SR-De	D-F	2.95	4.36	4.39	1.58	1.58	1.76
% Contribution of selected taxa to the total species richness:		6.44	11.45	13.10								

C: presence of coral or carbonate concretions at sediment surface; CD: presence of coral or carbonate concretions at sediment subsurface; A: absence of coral or carbonate concretions on sediment; TG: trophic guild; LF: life style; AS: average similarity; AD: average dissimilarity; SR: surface; SS: subsurface; He: herbivorous; Om: omnivorous; mic: microfauna; mei: meiofauna; mac: macrofauna; De: deposit feeder; Dt: detritus feeder; Su: suspension feeder; Pr: predator; M: motile; D: discretely motile; S: sessile; F: free living; T: tubiculous; B: burrow-dwelling; •: contributions lower than 1.5 (AD) or 2.0% (AS).

**Table VI.** Breakdown of percentage contributions from SIMPER analysis for comparisons between “Depth Zones” (Qualitative data). The taxa listed contribute at least 2.0% for average similarity within groups (AS) or at least 1.5% for dissimilarity between groups (AD). Numbers in **bold** mark the most frequent species (above 0.50 of frequency of occurrence) in each site.

Taxa	Frequency of occurrence						Contribution (%)					
	n	Z1	Z2	Z3	TG	LF	Z1	Z2	Z3	Z1/Z2	Z1/Z3	Z2/Z3
	S	288	195	154			AS:	AS:	AS:	AD:	AD:	AD:
							17.6	20.3	17.7	83.2	83.7	82.4
<b>Sipuncula</b>												
	Sipuncula und.	<b>0.66</b>	<b>0.70</b>	<b>0.81</b>	SR-Dt	D-F	10.01	13.02	21.66	1.53	1.53	1.63
<b>Annelida</b>												
Scolecida	cf. <i>Notomastus</i> sp.	0.42	0.33	0.38	SS-De	D-F	3.40	2.71	2.87	•	•	1.64
	Maldanidae und.	0.47	0.11	0.25	SS-De	D-T	4.39	•	1.78	•	1.53	•
	<i>Ophelina abbranchiata</i>	0.16	0.48	0.38	SS-De	M-F	•	5.83	3.67	1.52	•	1.87
	<i>Levinsenia</i> spp.	0.42	0.41	<b>0.56</b>	SR-De	D-B	3.76	3.53	10.20	1.51	1.75	2.02
	<i>Paradoneis</i> spp.	<b>0.50</b>	0.37	0.25	SR-De	D-B	5.15	3.26	•	1.56	1.54	1.57
Canalipalpata	<i>Laubieriopsis brevis</i>	0.11	0.41	0.06	SR-De	D-B	•	4.48	-	•	•	1.58
	<i>Laubieriopsis cabiochi</i>	0.21	0.15	0.44	SR-De	D-B	•	•	6.24	•	1.55	1.76
	<i>Spiochaetopterus bergensis/typicus</i>	0.37	0.22	0.38	SR-Su	S-T	2.76	•	2.95	•	•	1.51
	<i>Prionospio</i> spp.	0.24	0.11	0.44	SR-De	D-T	•	•	3.99	•	•	•
Errantia	Syllinae und.	0.45	0.19	0.19	SR-Pr-mei	M-F	4.03	•	•	•	•	•
	<i>Glycera lapidum</i>	0.42	0.48	0.31	SS-Pr-mac	M-F	2.97	5.74	1.70	1.56	•	1.80
	<i>Paradiopatra</i> cf. <i>hispanica</i>	<b>0.71</b>	<b>0.70</b>	<b>0.56</b>	SR-Om-mac	D-T	11.87	13.51	8.09	•	1.72	1.98
Oligochaeta	Oligochaeta und.	0.21	0.04	0.31	SS-Om-mic	M-F	•	-	2.15	•	•	•
<b>Arthropoda</b>												
Cumacea	Leuconidae spA	0.11	0.37	-	SR-He-mic	M-F	•	3.08	-	•	•	•

Table VI. Continued.

Taxa	Frequency of occurrence						Contribution (%)					
		Z1	Z2	Z3			Z1	Z2	Z3	Z1/Z2	Z1/Z3	Z2/Z3
	n	38	27	16			AS:	AS:	AS:	AD:	AD:	AD:
	S	288	195	154	TG	H	17.6	20.3	17.7	83.2	83.7	82.4
<b>Arthropoda</b>												
Tanaidacea	<i>Atlantapseudes nigrichela</i>	0.47	<b>0.59</b>	<b>0.63</b>	SR-Dt	D-F	5.20	9.87	10.10	1.68	1.71	1.93
	<i>Sphyrapus malleolus</i>	0.34	0.33	0.19	SR-Dt	D-F	2.38	2.91	•	•	•	1.50
Amphipoda	<i>Harpinia</i> spB	0.21	0.15	0.38	SR-Pr-mei	M-B	•	•	3.27	•	•	•
	<i>Harpinia</i> spC	0.24	0.44	0.13	SR-Pr-mei	M-B	•	3.97	•	•	•	1.58
	<i>Liropus elongatus</i>	0.34	0.07	0.13	SR-He-mic	M-F	2.28	•	•	•	•	•
<b>Mollusca</b>												
Bivalvia	<i>Abra longicallus</i>	0.39	0.41	0.31	SR-De	D-F	3.08	3.97	2.61	1.50	•	1.73
% Contribution of selected taxa to the total species richness:		7.29	10.77	12.99								

Z1: depth zone 1 (<540 m depth, top of the scarp); Z2: depth zone 2 (540-640 m depth, scarp); Z3: depth zone 3 (>640 m depth, base of the scarp); TG: trophic guild; LF: life style; AS: average similarity; AD: average dissimilarity; SR: surface; SS: subsurface; He: herbivorous; Om: omnivorous; mic: microfauna; mei: meiofauna; mac: macrofauna; De: deposit feeder; Dt: detritus feeder; Su: suspension feeder; Pr: predator; M: motile; D: discretely motile; S: sessile; F: free living; T: tubicolous; B: burrow-dwelling; •: contributions lower than 1.5 (AD) or 2.0% (AS); -: null contributions.