Universidade de Aveiro Departamento de Biologia
2017

MARIANA DIAS ALMEIDA

COMUNIDADES SUPRABENTÓNICAS DO MEDITERRÂNEO BATIAL: INFLUÊNCIA DE FACTORES AMBIENTAIS NA DIVERSIDADE E ESTRUTURA DA COMUNIDADE

DEEP-SEA SUPRABENTHOS ACROSS THE MEDITERRANEAN: THE INFLUENCE OF ENVIRONMENTAL DRIVERS ON BIODIVERSITY AND COMMUNITY STRUCTURE

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Tese apresentada à Universidade de Aveiro para cumprimento dos requisitos necessários à obtenção do grau de Doutor em Biologia, realizada sob a orientação científica da Professora Doutora Maria Marina Ribeiro Pais da Cunha, Professora Auxiliar do Departamento de Biologia da Universidade de Aveiro e co-orientação do Doutor Joan Baptista Claret Company, Investigador Sénior do Institute of Marine Sciences, Espanha e do Doutor Nikolaos Lampadariou, Investigador do Hellenic Center for Marine Research, Grécia.

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o júri

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Ao Mário. Aos meus pais, que não puderam estudar.

A título introdutório relativamente a este trabalho:

Quem dá o que tem, a mais não é obrigado
(Provérbio Português)

palavras-chave

Canhões submarinos; Mar Mediterrâneo; Comunidades suprabentónicas; Biodiversidade; Mar profundo; Oligotrofia

resumo

O mar Mediterrâneo batial apresenta características homeotérmicas (~14°C) e um gradiente de oligotrofia, que se acentua de oeste para este, de grande interesse para estudos de distribuição da fauna em mar profundo. Encontram-se também presentes outras condições específicas, de que são exemplos os processos oceanográficos e topográficos, que determinam variações ambientais nas suas diferentes regiões. Em particular, destaca-se o noroeste do Mediterrâneo cuja influência de canhões submarinos favorece uma maior produtividade e pressão antropogénica, que se traduz numa relevante atividade de pesca de arrasto em mar profundo. Embora pouco investigada, a macrofauna que habita acima do sedimento, designada por suprabentos, é uma componente importante da fauna bentónica com relevância nas cadeias tróficas de mar profundo. Neste contexto, foram estudadas as comunidades suprabentónicas ao longo de um gradiente oligotrófico (600-3000m; região oeste; mar Baleárico; centro, mar Jónico; este, Sul de Creta) e num canhão submarino e talude adjacente (400-2250m; noroeste do Mediterrâneo, mar da Catalunha) com o objetivo de caracterizar a biodiversidade, abundância e a estrutura da comunidade em relação com as variáveis ambientais. Em cada um dos locais, obtiveram-se amostras em três níveis da coluna de água acima do sedimento (10-50cm, 55-95cm e 100-140cm), de modo a caracterizar a distribuição vertical da macrofauna suprabentónica.

Este estudo identificou 232 taxa e 18 grupos tróficos, evidenciando-se os anfípodes e os cumáceos com um maior número de espécies. Os grupos mais abundantes foram os anfípodes, sobretudo predadores de zooplâncton, e os misidáceos seguidos dos isópodes, ambos maioritariamente omnívoros. A análise da distribuição vertical da macrofauna revelou uma diminuição acentuada na sua densidade do nível mais próximo do sedimento (10-50cm) para os níveis superiores. A estrutura da comunidade apresentou variações relacionadas com diversos fatores ambientais tais como, a quantidade e qualidade do alimento, o hidrodinamismo (associado a condições típicas do canhão) e a estrutura das massas de água. Os resultados mostram que as densidades apresentaram uma grande amplitude (3.5-538.9 ind.100m^{-2}) tendo os valores máximos sido registados no canhão de Blanes e no talude adjacente a cerca de 900m de profundidade. O número de espécies e o índice de diversidade de Shannon variaram entre os 21 e 84 e entre 1,28 e 3,35, respetivamente, tendo sido registada a menor diversidade no canhão submarino. Ao longo do gradiente de oligotrofia, de oeste para este, verificou-se um decréscimo das densidades e do número de espécies e constatou-se uma diminuição da abundância relativa de grupos que se alimentam no sedimento, em paralelo com o aumento da abundância relativa de grupos que se alimentam na coluna de água. Estes resultados foram associados a uma diminuição da matéria orgânica nos sedimentos da área mais oligotrófica. A distribuição estratificada variou ao longo do gradiente longitudinal, o que parece refletir a dinâmica das espécies (e.g. mobilidade, capacidade de dispersão, alimentação), as diferentes respostas das espécies à variabilidade nas condições abióticas, possíveis barreiras à dispersão e ao gradiente de oligotrofia, resultando em valores elevados de β-diversidade. A noroeste, no canhão de Blanes, a estrutura da comunidade parece ser condicionada pela maior quantidade e diversidade de fontes de matéria orgânica indicada pela presença de predadores no sedimento e de detritívoros no talude adjacente. Nas zonas do canhão mais próximas da influência terrestre, a estrutura e a biodiversidade da macrofauna suprabentónica parecem estar relacionadas com a variabilidade temporal das condições hidrodinâmicas, em particular, no aumento da intensidade de correntes e de fluxo de partículas que ocorre no outono e no inverno (descargas do rio e tempestades). Nestas condições, verificou-se o aumento da densidade e a redução da biodiversidade, possivelmente devido a uma maior presença de omnívoros com elevada mobilidade (ex. misidáceos). No talude adjacente, caracterizado por menor perturbação natural e maior qualidade de matéria orgânica de origem pelágica, a comunidade reflete uma diversidade elevada, em especial, na primavera. A maior profundidade, observou-se uma diversidade similar no canhão e no talude, provavelmente devido a condições de inferior perturbação natural e menor influência da ação do canhão. No entanto, após a ocorrência de um processo energético de grande intensidade, como o efeito de cascata de massas de água de elevada densidade (ex. 2012), verificou-se um aumento considerável do número de espécies e das densidades no canhão e no talude. Este aumento pode dever-se a um incremento de matéria orgânica fresca no talude inferior e na bacia do Mediterrâneo. Apesar da resiliência das comunidades suprabentónicas, a sua diversidade parece ser afetada pela elevada e continuada perturbação causada pela pesca de arrasto.

Concluindo, neste trabalho existem evidências de que as diferentes regiões analisadas apresentaram elevada variabilidade na composição, estrutura e biodiversidade, que se atribui à heterogeneidade de grupos tróficos e modos de vida do suprabentos. Os valores de β-diversidade observados foram atribuídos à disponibilidade de alimento, heterogeneidade do habitat e perturbação natural. Os resultados deste estudo evidenciam a necessidade de considerar os mesmos elementos faunísticos na composição teórica da fauna que vive na interface coluna água/sedimento para comparação com outras regiões. Estudos de auto-ecologia e interações bióticas e, finalmente, a necessidade de amostragem replicada, são também aspetos a considerar para uma melhor compreensão das comunidades de suprabentos.

Recomenda-se, por fim, dada a relevância funcional das comunidades suprabentónicas, a inclusão deste compartimento bentónico em futuros estudos focados no funcionamento dos ecossistemas de mar profundo.

keywords

Submarine canyons; Mediterranean Sea; Suprabenthos; Biodiversity; Deep-sea; Oligotrophy

abstract

The Mediterranean Sea is characterized by homeothermia (~14ªC) and a gradient of increasing oligotrophy from west to east which makes it of particular interest to study distribution patterns of deep-sea fauna. Particular oceanographic processes and topographic characteristics vary in different regions. The northwestern Mediterranean, where the shelf is deeply incised by numerous submarine canyons, is typically more productive and it is also subjected to an intense anthropogenic pressure mainly by deep-sea bottom-trawling fisheries.

The suprabenthos, loosely defined as the macrofauna living in the sediment/water column interface, is an important component of the benthic fauna, with a relevant role in deep-sea food webs, albeit poorly investigated. In this context, suprabenthic assemblages were studied along an oligotrophic gradient (600-3000 m water depths; western region, Balearic Sea; central region, Ionian Sea; eastern region, South of Crete) and in a submarine canyon and adjacent slope (400-2250 m; northwestern Mediterranean Sea, Catalan Sea) aiming to examine their biodiversity, abundance and community structure in relation to varying environmental conditions. In each sampling site, samples were collected at three water layers above the sediment (10-50 cm; 55-95 cm; 100-140 cm), allowing to characterize the vertical distribution in the close vicinity of the seafloor.

The specimens collected were ascribed to 232 taxa, from which amphipods and cumaceans were the most species-rich groups. Amphipods, mostly predators on zooplankton, followed by mysids and isopods, mostly omnivores, were the most abundant groups. The analysis of the near-bottom vertical distribution of the suprabenthic fauna showed a marked decreased in densities from the layer closer to the sediment (10-40 cm water layer) to the upper layers. Community structure varied in relation to environmental variables such as food input, hydrodynamic regime, topographic features (e.g. canyon-associated conditions) and properties of the water masses. The general results showed high variability in densities (3.5-538.9 ind.100 m^{-2}) with maximum values registered in the Blanes Canyon and adjacent slope at 900 m depth. The number of species and the Shannon biodiversity index varied from 21 to 84 and from 1.28 to 3.35, respectively, with the lowest biodiversity observed in the canyon.

Along the longitudinal gradient, densities and number of species decreased, the relative abundance of animals relying on food sources from the sediment decreased in parallel with an increase in the relative abundance of animals feeding on the water column. These results likely reflect the low organic matter input to the sediments in the more oligotrophic region. The near-bottom vertical distribution of the fauna changed along the longitudinal gradient, which may be associated to the functional traits of the species (e.g. motility, dispersion capability, feeding mode), to the different responses of individual species to changing abiotic conditions, the occurrence of topographic barriers and to the oligotrophy. These changes in the composition of the suprabenthic assemblages maintained similar values of α-diversity across the longitudinal/oligotrophy gradient, but resulted in high turnover (β-diversity).

In the northwestern region the community structure appeared to be driven by the quantity and quality of food sources, revealed by the presence of surface predators in the Blanes Canyon and adjacent slope and also detritivores in the latter environment. In the canyon head and upper reaches, the community structure and biodiversity appeared to be driven by the temporal variability in hydrodynamic conditions with increased intensity of currents and particle fluxes in autumn and winter (river discharges, storms). Under disturbance conditions, densities increased and biodiversity decreased due to the dominance of omnivores with high motility (e.g. mysids). In the slope, the assemblages appeared to respond to the lower particle fluxes but higher quality of the predominantly pelagic organic input, by showing an increased biodiversity, particularly in spring. At deepest sites, biodiversity was similar between canyon and open slope, probably owing to the lower intensity of natural disturbance and lessening of a putative canyon effect. Nevertheless, after the occurrence of high energetic processes, such as a dense shelf cascading event (e.g. in 2012), an important increase in the number of species and densities was observed both in the canyon and slope, probably reflecting the increment of fresh organic matter in the lower slopes and basin. Despite the overall high resilience of suprabenthic assemblages, they were affected by high and continued trawling disturbance.

In conclusion, this Thesis showed evidence of highly variable patterns in the composition, biodiversity and structure of the suprabenthic assemblages typified by the occurrence of a variety of trophic groups and life styles. High levels of spatial and temporal turnover in species composition was attributed to food availability, habitat heterogeneity and natural disturbance.

In order to improve the knowledge on deep-sea suprabenthos, more studies on its auto-ecology and biotic interactions are needed. Also important to enable biogeographical and even regional comparisons, is to reach a consensus on a standardized terminology and conceptual definition concerning this faunal compartment, as well as to improve the spatial and temporal replication of sampling. Finally, given the important functional role of suprabenthos in marine food webs, it is strongly recommended to include this benthic compartment in future studies focusing on deep-sea ecosystem functioning.

Declaro que esta tese é integralmente da minha autoria, estando devidamente referenciadas as fontes e obras consultadas, bem como identificadas de modo claro as citações dessas obras. Não contém, por isso, qualquer tipo de plágio quer de textos publicados, qualquer que seja o meio dessa publicação, incluindo meios eletrónicos, quer de trabalhos académicos.

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SECTION 1. INTRODUCTION

1.1 General background

The deep sea is the area of the ocean below the shelf break, at 200 m depth, covering approximately 63% of the Earth's surface area and with an average depth of approximately 3.8 km (Tyler, 2003). The deep seafloor can be divided in several zones based on depth and on ecological aspects (Fig. 1.1): the continental slope encompasses the bathyal zone (approx. 200-3000 m) characterized by a steep slope of the seafloor (at an average angle of about 4°); the abyssal zone includes the gentler slope of the continental rise (approx. 3000-4000 m) and the abyssal plain (4000-6000 m), mainly a flat area covering the largest area of the ocean floor; and the hadal zone comprising the deep trenches (6000 to 11000 m) (Gage and Tyler, 1991; Levin and Sibuet, 2012).

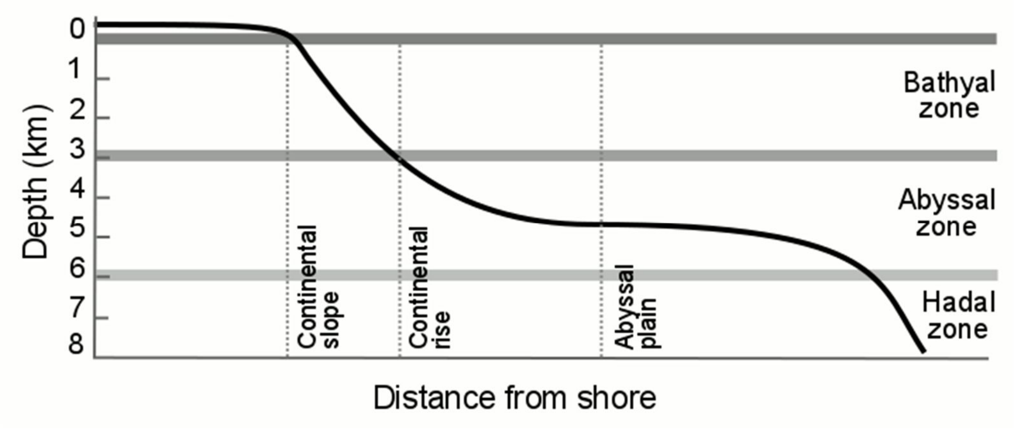

Figure 1.1 Diagrammatic cross section of the ocean floor showing the major topographic features and depth zones. The subittoral zone is not labelled. Modified from Gage and Tyler (1991).

In terms of volume, the majority of the deep sea is the water column above the seafloor, the pelagic environment, less known than the benthic environment, owing to the huge dimension of the deep-pelagic zone and to the difficulty of sampling the highly mobile and widly dispersed pelagic assemblages (Ramirez-Llodra et al., 2010).

The deep seafloor is far from being monotonous as it was once assumed. Instead, it is characterized by high habitat heterogeneity. Specific physiographic and oceanographic conditions create a variety of habitats (e.g. canyons, seamounts, cold water corals, hydrothermal vents), mostly concentrated in the continental margins, mid-oceanic ridges and trenches, and which shelter a wide variety of microbial and faunal assemblages (Ramirez-Llodra et al., 2010). Deep-sea habitats harbour the largest reservoirs of biomass and non-renewable resources (e.g., gas hydrates and minerals) (Gage and Tyler, 1991). Moreover, there is accumulated evidence that the biodiversity is extremely high (Rex and Etter, 2010) and promote ecosystem processes and functions with a fundamental role to the functioning of the biosphere (Danovaro et al., 2008a). Therefore, the knowledge of the biodiversity and its relationships with deep-sea ecosystem functioning is crucial to understanding the response of these ecosystems to disturbance. However, despite all the research in the last decades and the notable technological advances, only a small portion of this biome has been investigated in detail (Ramirez-Llodra et al., 2010; Danovaro et al., 2014). More recently, the application of new technologies (e.g. ROVs, AUVs, landers, multibeam echosounders) allowed to carry out the first manipulative experiments on seafloor communities, to extend habitat mapping to extreme environments, to test ecological hypothesis and to begin to quantify the abundance of pelagic life (Danovaro et al., 2014).

1.1.1 Major environmental characteristics of the deep sea

In the ocean the light that supports photosynthesis only can penetrate until 150-200 m depth (called the compensation depth). From this level to 1000 m (designated as the disphotic zone), light penetration does not allow photosynthesis to be performed with enough efficiency to sustain life. Below this level, lies the zone with total absence of light (designated as the aphotic zone) (Lalli and Parsons, 1993). Surface productivity is therefore the base of the food chain that sustains life in the deep sea. The exception to this, is primary production based on chemosynthesis, which supports life in localized deep-sea systems such as hydrothermal vents, seeps and subsurface biosphere. The scarcity of food input down the water column and in the deep seafloor has profound consequences to the ecology of organisms living in the deep sea (Thistle, 2003). This is among the most food-limited ecosystems on the globe (Smith et al., 2008), yielding relatively low rates of growth, reproduction, respiration, recolonization and sediment mixing (Gage and Tyler, 1991).

Pressure increases at a rate of approximately 1 atm (100,000 Pa) every 10 m of water depth and imposes a specialized fauna adapted to this extreme condition. Increase pressure affects organisms physiologically (e.g. compression of gas-filled spaces) and biochemically (e.g. performance of enzymes and lipid structures changes with pressure (Kaiser et al., 2011; Somero, 1992).

Water temperature at the deep seafloor is generally constant and subjected to only little variation according to the latitude and region (Mantyla and Reid, 1983). In the mesopelagic zone, the water temperature declines rapidly, creating a steep temperature gradient known as the permanent thermocline. Beneath this level, at around 800 m, there is no seasonal variation and the temperature is typically between 4 ºC to -1Cº, except in some regions like the Mediterranean Sea and the Red Sea, with values around 13ºC and 21.5ºC, respectively (Gage and Tyler, 1991). Deep-sea organisms must be adapted to the effects of low temperatures, such as the reduction of enzyme flexibility and metabolic rates (Hochachka and Somero, 1984). Such adaptations to low temperatures may constitute a dispersal barrier for organisms between colder (deeper) and warmer waters.

Water salinity is also relatively constant, around 35 psu, with some exceptions including the Mediterranean and Red seas, with values around 39 psu (Gage and Tyler, 1991). Variations in salinity in the deep-sea habitats appears to be irrelevant to the ecology of deep-sea organisms (Thistle, 2003).

Oxygen enters the ocean by exchange with the atmosphere and as a result of photosynthesis by marine autotrophic organisms in the euphotic zone; it reaches the deep seafloor through the exchange of the water masses (Thistle, 2003). With some exceptions, the oxygen in deep waters is near saturation (5-6 $ml.l^{-1}$) (Thistle, 2003). Oxygen consumption is lower when compared to other marine ecosystems because of the lower abundances of organisms and low temperatures in the deep (Nybakken and Bertness, 2005). However, in mid-water oxygen minimum zones associated to strong upwelling regions, and in areas where bottom water does not freely exchange (e.g. because of a topographic barrier), oxygen concentration can be much lower (OMZs; $O_2<0.5$ ml l^{-1}) than in the surrounding regions (Thistle, 2003). Such conditions can reduce benthic diversity and lead to specific adaptations to hypoxia (Levin et al., 2009).

Hydrodynamic conditions and topographic characteristics are important factors shaping the seafloor and affecting the benthos that lives within. In general, currents in the deep sea are non-erosive (10 $cm.s^{-1}$ in the bathyal zone at one meter above the bottom and less than 4 $cm.s^{-1}$ in the abyssal zone) and current velocity varies little from day to day at a location (Eckman and Thistle, 1991). During periods (e.g. benthic storms) or in locations (e.g. submarine canyons) of fast flow, intense near-bottom currents (>15 $cm.s^{-1}$) are able to resuspend and redistribute sediments, which strongly influence the nature of deep biota, both positively and negatively (Aller, 1989; Company et al., 2008; Mcclain and Barry, 2010; Romano et al., 2013). For instance, higher current velocities (30 $cm.s^{-1}$) may benefit the benthic animals by increasing horizontal food flux input. On the other hand, increased flow may prevent sediments and organic material from settling, leading to a decrease in food availability for the benthos and strong currents may also erode the sediment and impact the benthos, particularly small-sized and/or low biomass organisms (Thistle, 2003).

Deep-sea sediments, typically fine grained, are derived from the supply of terrigenous particles and by biological particles produced by planktonic organisms in the euphotic zone (Gage and Tyler, 1991). The balance between the rates of supply of terrestrial and biogenic particles and the rate of dissolution of the latter controls the local sediment composition (Thistle, 2003). At a small spatial scale, heterogeneity in the sediment is caused by bioturbation (e.g. organisms by building tubes, tests, and mudballs) and by other environmental sources of disturbance creating patchiness in the deep seafloor sediment texture and food content, and influencing species distribution and community composition (Grassle and Sanders, 1973; Grassle and Morse-Porteous, 1987; Thistle, 2003).

1.1.1.1 Productivity

Most of the deep sea is a heterotrophic system (metabolism reliant on breakdown of complex organic molecules; Gage, 2003); it is also considered an allochthonous system, depending mostly on organic material sinking to the deep ocean basins from primary photosynthetic production in the euphotic zone (Fig. 1.2).

Particulate organic matter (POM), the main source of organic carbon to the deep ocean, enters the deep sea in the form of terrestrial and plant remains, carcasses of nektonic organisms and small remains of plankton (faecal pellets, moults, phytodretitus) (Gage and Tyler, 1991). During the descent through the water column, it can aggregate in larger particles increasing size with increasing depth, forming the marine snow (Gage, 2003). The downward vertical flux of POM decreases rapidly with increasing water depth due to the water column conditions and consumption by resident biota, mostly occurring at the upper 500 m of the water column (Gage, 2003). That is to say that only a small fraction (1-3%) of the production of the surface layers arrives to the seafloor (Gage, 2003) and therefore the deep sea is considered an extreme food limited environment (Smith et al., 2008). Aggregations of sunken wood and marine mammal falls may provide abundant but localized and relatively ephemeral food availability (Ramirez-Llodra et al., 2010). Other source of input of organic matter to the deep is promoted by several groups of organisms which perform vertical diel migrations (DVM community). By feeding during the night in the surface layers and returning to the deep during day-time, they actively transport material (as a result of their metabolic activity), resulting in downward fluxes of carbon (Longhurst and Harrison, 1988). Another process of organic matter input is the lateral advection of dissolved organic matter (DOM), from adjacent areas of the deep seafloor, which takes place in the benthic boundary layer (BBL) and in productive areas, such as canyons. Lateral transport of particles is controlled by changes in flow dynamics and resuspension, and lateral transport of organic flux (Gage, 2003).

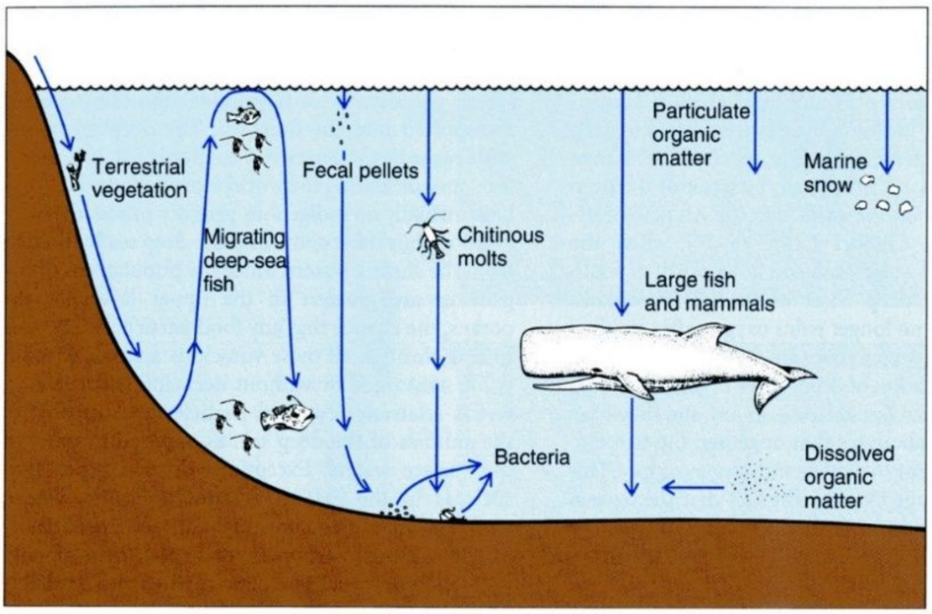

Figure 1.2 Schematic representation of the various food sources for the deep-sea. Modified from Nybakken and Bertness (2005).

1.1.1.2 Temporal variability

The arrival of organic matter to the deep sea is subjected to variation driven by the annual cycle of primary production (e.g. impulses of sinking phytodetritus with peaks in spring/early summer and later in autumn) or inter-annual shifts in primary production (e.g. El Niño/El Niña events). Several studies suggested that all benthic components (from bacteria to megafauna) respond to the POC flux from the photic layer (e.g. Billet et al., 1983; Gooday, 2002). Sedimentation pulses of organic matter to the deep sea may vary in intensity between years, are often unpredictable and can be caused by benthic storms, canyon sediment transport (Thistle et al., 1991; Company et al., 2008; Glover et al., 2010), atmospheric driven events (Canals et al., 2006) or episodic falls of large mammal carcasses (Smith and Baco, 2003) or sunken wood (Bienhold et al., 2013). The study of how deep-sea animals are adapted to the scarcity of food and how they react to seasonal, inter-annual and decadal-scale refuel processes is one of the main topics in marine ecology.

1.1.2 Biodiversity in the deep sea: general considerations

The study of the deep-sea benthic fauna started historically in the Mediterranean Sea with Edward Forbes, who dredging down to 420 m depth in the Aegean Sea (H. M. S. Beacon, 1841–1842) found very few organisms and postulated the “Azoic Theory”, stating that “no life exists in the oceans below ca. 600 m” (Forbes, 1844; Anderson and Rice, 2006). He based his theory on samples collected in a highly oligotrophic area, where life is indeed sparse (Fredj and Laubier, 1985; Dugdale and Wilkerson, 1988). However, his theory was rejected by the accumulated evidence from increasing deep-sea sampling. The great oceanographic expeditions in the nineteen century (e.g. H. M. S. Challenger in 1872-1876), in the 1950’s (Danish round-the-world Galathea expedition in 1950-52) and the discovery of high species richness at the slopes of the Atlantic Ocean in the 1960’s and 1970’s (Hessler and Sanders, 1967) have changed this paradigm. Since then, more studies indicate that deep sea supports high biodiversity (Hessler and Sanders, 1967; Grassle and Maciolek, 1992; Etter and Mullineaux, 2001; Snelgrove and Smith, 2002; Stuart et al., 2003), mainly of small detritivores inhabiting the sediments. Indeed, Sanders (1968) suggested that the deep sea supports a higher species diversity than shallow waters and proposed the stability–time hypothesis i.e. the deep sea is a stable and unchangeable environment leading to a large number of specialized species with narrow niches (Snelgrove and Smith, 2002). This assumption was debated by other authors (Gray, 1994; Gray et al., 1997; Gray, 2001; Lambshead et al., 2003) who questioned the differences between shallow and deep-sea biodiversity and the mechanisms responsible for maintaining high diversity (Snelgrove and Smith, 2002). Over the years, several other theories such as the habitat heterogeneity hypothesis (Sanders, 1968, 1969), the biological disturbance hypothesis (Dayton and Hessler, 1972), the intermediate disturbance hypothesis (Connell, 1978), the dynamic equilibrium model, the patch dynamic model (Grassle and Sanders, 1973) have been proposed to explain the deep-sea diversity, but no single theory can explain all the observed diversity patterns at all scales.

Nevertheless, there is a common agreement that the deep sea is not a physically stable environment but is subjected to various degrees of physical heterogeneity, disturbance and productivity regimes which supports high biodiversity (McClain and Schlacher, 2015).

Deep-sea biodiversity is generally characterized by low dominance and high evenness (usually measured by the Pielou index, J; between 0.7 and 1) associated to more stable benthic assemblages, capable of optimizing the limited food resources (Gage and Tyler, 1991; Ramirez-Llodra et al., 2010). However, in areas with strong gradients of environmental factors, such as chemosynthetically-driven and canyon systems (Van Dover, 2000) and in OMZs (Levin et al., 2009) low diversity and high dominance may be observed.

The advances in sampling technology and increasing deep-sea sampling efforts since the 1950's, lead to a better description of deep-sea abundance and diversity patterns. A general pattern assumed in the deep sea is the exponential decrease in benthic metazoan abundance, biomass, and also body size, with depth, as a consequence of the decreasing surface production and POM flux with increasing depth and distance from the coast (Rowe, 1983; Rex et al., 2006). The bathymetric gradient is more marked in oligotrophic regions by interregional comparisons (e.g. depressed standing stock in the Arctic Sea (Kröncke et al., 2000) and in the Mediterranean Sea (Tselepides et al., 2000a). Areas of upwelling and lateral transport (Blake and Hilbig, 1994; Galeron et al., 2009), with regimes of strong near-bottom currents (Aller, 1997) or proximity to OMZs (Levin, 2003) as well as bottom topography (e.g. trenches, Gambi et al., 2003; submarine canyons, Vetter et al., 2010) generally have enhanced abundances often coupled with depressed biodiversity.

Other two global deep-sea diversity patterns are generally assumed: a diversity decrease from equatorial to polar regions and the unimodal relationship between diversity and depth (Rex and Etter, 2010 and references therein). Depressed diversity towards the poles is known for some macrofaunal groups in the north Atlantic Ocean and is manifested by an increase in dominance observed in some taxa, induced by high and seasonal nutrient loading (Rex et al., 2000) however their existence is not consistent across all oceans or regions (Lambshead et al., 2000; Rex et al., 2001). Particular taxa show a different or no trend (Rex et al., 1993; Crame, 2000; Lambshead et al., 2000) and this pattern is not evident in the South Atlantic Ocean (Stuart et al., 2003). Patterns of biodiversity at these very large scales are also likely influenced by evolutionary-historical phenomena (Stuart et al., 2003).

Bathymetric gradients of species diversity are the most studied in the deep-sea benthos and appear to be related to food supply. Diversity shows a parabolic distribution with depth, particularly in the north Atlantic Ocean, with the peak generally occurring at intermediate bathyal depths (Rex, 1981; Grassle and Maciolek, 1992) and low diversity at the upper bathyal and abyssal depths, with variation in the depth at which the peak in diversity is reached and depending on the taxa investigated (Stuart et al., 2003). Depressed biodiversity coupled with high density at the upper bathyal depths appears to be related to high nutrient loading (Rex, 1981); at abyssal depths, diversity is probably depressed by vulnerability to the Allen effect (Rex et al., 2005). Unimodal patterns, however, are not universal as they are strongly influenced by other ecological processes (Stuart et al., 2003). Changes in oceanographic conditions, at specific depths, often modify bathymetric horizontal diversity trends (e.g. Levin and Gage, 1998; Vetter and Dayton, 1999) which may also vary among taxa and geographic region (Flach and de Bruin, 1999; Tselepides et al., 2000a; Stuart et al., 2003).

The species turnover (also designated as β-diversity), is especially evident along depth gradients in the deep-sea (Carney, 2005). Species turnover is observed at a higher rate in the steeper bathyal zone: at the shelf-slope transition (300–500 m), along the upper slope (1000 m), and at a lower-slope transition zone (2000–3000 m) due to marked changes in environmental factors (Carney, 2005). It appears that the changes associated with these depth ranges are determined by the interaction of biological traits (e.g. predation, competition, dispersion), larvae dispersal and environmental influences (e.g. absence of light, high hydrostatic pressure, low temperature, oxygen minimum zone, water masses, nature of the substrate and food availability) which constrain species distributions along the depth gradient (Carney, 2005; Rex and Etter, 2010).

The observed variation in biodiversity results from the influence of both ecological and evolutionary processes, that operate at different spatial and temporal scales (Etter and Mullineaux, 2001; Levin et al., 2001; Snelgrove and Smith, 2002; Mcclain and Barry, 2010). Smaller-scale processes are embedded hierarchically within larger-scale processes, and tend to occur at faster rates. At a large scale, physical processes are the main factors that regulate the distribution of benthic parameters, whereas at the local scale, the complex biological interactions within the food web dominate.

Species diversity at local scales is controlled by small-scale processes involving resource partitioning, competitive exclusion, predation, facilitation, physical disturbance, recruitment, and physiological tolerances, all of which are mediated by the nature and degree of heterogeneity (Levin et al., 2001). At regional scales, dispersal, metapopulation dynamics, gradients in habitat heterogeneity and several environmental gradients such as sediment grain size, productivity, bottom-water oxygen concentration, flow and disturbance, are important (Levin et al., 2001). At global scales, large-scale disturbance and speciation/extinction rates are indicated as the fundamental processes regulating species diversity (Levin et al., 2001). Some or all of these factors can act in different combinations and can be superimposed onto other local or regional conditions, causing a variety of biotic responses (Levin et al., 2001).

1.1.2.1 Sedimented slopes: a general overview

Continental margins correspond to a small fraction of the ocean global area but account for a disproportionately large fraction of the ocean global primary production (10-15%), nutrient recycling, carbon burial (>60% of total settling organic carbon) and fisheries production (Muller-Karger et al., 2005). The slopes are the steeper part of the continental margins and connect the shelf to the deep basins; all the exchanges of water, energy and matter, including sediment, organisms and contaminants, between these two domains, occur through the slopes (Danovaro et al., 2009b; Levin and Sibuet, 2012).

Continental slopes are characterized by irregular topography, high sediment heterogeneity and interaction of different water masses and are therefore subjected to a broad range of drivers, including highly variable flux of materials, down-shelf cascades, sediment slumps, turbidity currents, benthic storms and organic inputs from river and canyon systems (Glover et al., 2010). A variety of deep-sea habitats occur at slopes that are also characterized by high genetic and species diversity (Levin et al., 2010; Ramirez-Llodra et al., 2010). Moreover, enhanced levels of biodiversity on continental slopes systems (e.g. the peak of the unimodal diversity depth pattern described above) have been considered as a source of diversity for both shelves and deeper basins through radiation and dispersal processes (i.e. source-sink hypothesis, Rex et al., 2005).

Continental margin ecosystems provide important goods and services (e.g. energy, mineral resources, fisheries, disposal of sewage and mine tailings) and subsequently the human footprint on these ecosystems is increasing, often in areas where faunas and habitats are unstudied (Ramirez-Llodra et al., 2011; Levin and Sibuet, 2012). For example, exploitation of deep-water fisheries has increased since the 1960´s, and progressively reached deeper waters. It is currently known that deep-sea trawling has an impact on fish populations and by-catch species down to 3100 m (Devine et al., 2006; Bailey et al., 2009). Overfishing is particularly detrimental to deep-sea species which are often long lived with slow growth and delayed maturity (e.g. orange roughy) (Morato and Clark, 2007), making them poorly adapted to endure heavy fishing pressure (Ramirez-Llodra et al., 2011). The effects of trawling are also severe in the deep-sea benthic habitat and communities, especially on the upper continental slope and seamounts (Gage et al., 2005; Clark and Koslow, 2007), by reducing the diversity and biomass of benthic invertebrates, destructing cold-water corals (e.g. Hall-Spencer et al., 2002) and altering the structure of the assemblages (e.g. by removing sessile epifauna) (Ramirez-Llodra et al., 2009). Furthermore, several studies have shown that intense repetitive trawling on the slope and on canyon flanks can create significant disturbance in the sediment, causing sediment gravity flows and changes in canyon sediment dynamics and seafloor morphology, as well as major consequences for the assemblages (e.g. suffocation of cold-water corals by re-suspended sediments) (Palanques et al., 2006; Puig et al., 2012; Martín et al., 2014).

Biological communities (including cold-water corals) on sedimentary upper slopes, submarine canyons and seamounts are at higher risk as human impacts such as bottom fishing, oil and gas extraction, and sewage dumping increase (Ramirez-Llodra et al., 2011). It is therefore imperative to describe and quantify continental margin biodiversity and understand how margin geomorphological, hydrographic, geochemical, and biogenic heterogeneity influences α and β-diversity at multiple spatial and temporal scales (Ramirez-Llodra et al., 2010; Levin and Sibuet, 2012).

1.1.2.2 Submarine canyons: Biological patterns

Submarine canyons are valleys that incise the shelves and/or slopes; they occur worldwide, and vary in size, shape and morphological complexity. Because of their steep topography and difficult access, multidisciplinary studies necessary to understand their geologic, oceanographic and ecological significance have developed only in recent decades, in parallel with technological improvements (e.g. swath bathymetry, remote sensing, long-term moorings and ROVs) (Ramirez-Llodra et al., 2010).

Canyons are the primary conduits of sediment and organic matter to the abyssal plains and often provide localized areas of organic enrichment (Vetter and Dayton, 1999; de Stigter et al., 2007; Allen and Durrieu de Madron, 2009; Lopez-Fernandez et al., 2013b). Canyons provide various and complex physical habitats (e.g. canyon morphology, multiple types of substrates), often more than the surrounding slopes (Hargrave et al., 2004; Schlacher et al., 2007). Their extreme topography has consequences in diverse oceanographic processes such as internal waves, strong near-bottom current regimes, turbidity flows, dense shelf water cascading, which may be amplified by the presence of river sources (Puig, 2004; Canals et al., 2006; Zuniga et al., 2009; Durrieu De Madron et al., 2013).

This physical environment characterized by high heterogeneity, disturbance and productivity regimes creates unexpected high variation in biotic diversities (Levin et al., 2001; Harris and Whiteway, 2011). Organic enrichment in canyon floors is usually linked with high benthic densities and/or biomass when compared to those on adjacent slopes (Soetaert and Heip, 1995; Vetter and Dayton, 1998; Schlacher et al., 2007; De Leo et al., 2010; Cunha et al., 2011; Gunton et al., 2015) but occasionally opposite trends may be found due to frequent disturbance events (Garcia et al., 2007; Romano et al., 2013) or no influence is detected (Houston and Haedrich, 1984; Ramirez-Llodra et al., 2009; Bianchelli et al., 2010). Some canyons may present higher diversity than on the open slopes at equivalent depths (Ramirez-Llodra et al., 2009; Vetter et al., 2010) but in other cases high disturbance rates (Rowe et al., 1982) and sedimentary habitat instability leads to reduced diversity (Gage et al., 1995; Bianchelli et al., 2008). Some canyons are defined as “hotspots” of benthic diversity due to the presence of relevant levels of endemism and the occurrence of species with peculiar life-history patterns (Vetter et al., 2010; De Mol et al., 2011; Danovaro et al., 2014).

The complex ecological characteristics of canyons favour the occurrence of diversified food webs. Suspension feeders and highly mobile species take advantage from the accelerated currents and sedimentation (Shepard et al., 1974; Vetter et al., 2010), planktivores feed on zooplankton aggregations (Macquart-Moulin and Patriti, 1996), detritivores and deposit feeders consume enhanced organic deposits (Vetter and Dayton, 1999), scavengers feed on concentrated carcasses and plant remains (Bernardino et al., 2010). Some demersal and benthic species are also known to use canyons for nursery and spawning (Stefanescu et al., 1994).

Enhanced locally fishery production is often found in the canyon heads of shelf-incising canyons located close to coastal areas (Harris and Whiteway, 2011), and is attributed to the channelling effect concentrating detrital organic matter and pelagic animal populations in canyons (Vetter and Dayton, 1999; Ramirez-Llodra et al., 2008). Fishing activity and other anthropogenic pressures (e.g. contaminants) make submarine canyons more vulnerable marine ecosystems and thus particularly relevant to study.

1.1.3 The Mediterranean Sea

The Mediterranean Sea, one of the major peripheral seas, is characterized by fast circulation and small residence time (Bethoux et al., 1999), unique paleo-ecological, physiographic and environmental features, i.e. restricted exchanges with the open ocean, oligotrophy and homeothermy (Hopkins, 1985; Tyler, 2003; Danovaro et al., 2010). In addition, it is severely subjected to anthropogenic pressures, such as high density of inhabitants in the coastal areas and a long history of exploitation of marine resources; the Mediterranean bounded general water circulation renders its ecosystems particularly vulnerable to contamination and, more generally, to human impact and climate change (Coll et al., 2010; Ramirez-Llodra et al., 2011). The Mediterranean Sea is therefore a unique model to study several oceanographic processes that usually take a long time to occur in the Global Ocean (Bethoux et al., 1999) and to investigate patterns of deep-sea biodiversity and how they are affected by environmental and human-driven factors (Ramirez-Llodra et al., 2011).

1.1.3.1 Environmental characteristics

The Mediterranean Sea, situated at the crossroads of Africa, Europe and Asia, is the largest (2969000 km^2) and deepest (maximum 5267 m) peripheral sea on earth (Coll et al., 2010). It is a semi-enclosed sea with a natural connection to the Atlantic Ocean through the relatively narrow and shallow Strait of Gibraltar (400 m maximum water depth) in the west; through the Dardanelles Channel to the Sea of Marmara and the Black Sea in the northeast and through the Suez Canal to the Red Sea and the Indian Ocean in the southeast (Sardà et al., 2004) (Fig. 1.3). The Strait of Sicily, a narrow sill approximately 300 m water deep, divides the Mediterranean Sea in two depressions: the western (mean depth, about 1600 m) consisting of two basins, the Algero-Provençal basin and the Tyrrhenian Sea; and the central-eastern, consisting of three main deep basins: Ionian and Aegean seas and the Levantine basin.

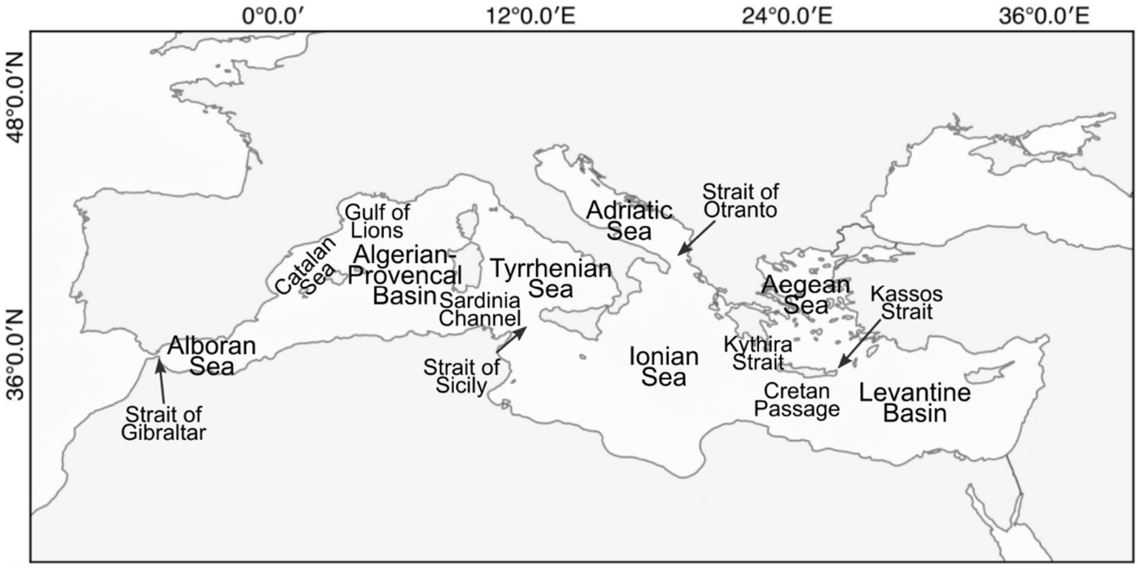

Figure 1.3 The Mediterranean Basin configuration. Modified from Demirov and Pinardi (2002).

The Mediterranean Sea has a narrow continental shelf (15% of the total area), with a shelf break at 100-110 m, and therefore its largest fraction is classified as deep sea. The bathyal zone, down to 3000 m depth, represents 72% of the total area compared to the 15% of the Word Ocean (3000- 5093 m) (Emig and Geistdoerfer, 2004). It has a mean depth of 1450 m, much shallower than the average depth of the world ocean (about 3850 m) and the deepest point, at 5121 m, is found at the North Matapan-Vavilov Trench in the Ionian Sea (Danovaro et al., 2010).

The seafloor of the continental slopes is mainly composed of fine-grained sediments with an increase in the biogenous fraction (pteropods, pelagic foraminiferans) with increasing depth (Emelyanov, 1977). The Mediterranean deep seafloor is composed by heterogeneous structures and complex sedimentological features i.e. open slopes, submarine canyons, seamounts, bathyal and abyssal plains with deposits of hemipelagic and turbidity muds, deep-hypersaline anoxic basins, cold seeps and mud volcanoes (Danovaro et al., 2010). A particular feature of the margins of the northwestern Mediterranean Sea is the presence of numerous submarine canyons, approximately 8.9% of all submarine canyons in the World (Harris and Whiteway, 2011; Canals et al., 2013). Therefore, submarine canyons are naturally one of the most relevant topographic features in the Mediterranean Sea with a high significance for the functioning of this land-locked basin (Canals et al., 2013).

Hydrology

The main hydrological features of the Mediterranean Sea are i) high homeothermy from 300-500 m to the seafloor, varying from 13.0 to 13.5°C in the western basin and from 13.5 to 15.5°C in the eastern basin (Hopkins, 1985); ii) high salinity, from about 38.0 to 39.5 psu, caused by high evaporation and low input from freshwater terrestrial waters and precipitation; iii) a microtidal regime; iv) high oxygen concentrations present across the water column down to the seafloor (except for specific locations such as the anoxic brine lakes in the central basin); v) a complex system of currents imposed by the Gibraltar and Sicily straits; and vi) oligotrophic conditions, with strong energetic gradients and low nutrient concentrations in the eastern basin (Danovaro et al., 2010) (Fig. 1.4). Some of the major abiotic characteristics of the Mediterranean Sea differ from the Atlantic Ocean where salinity is lower (36.5 psu), temperature decreases gradually with depth (to 2.5ºC at 3000 m) and productivity rates are higher (Tyler, 2003).

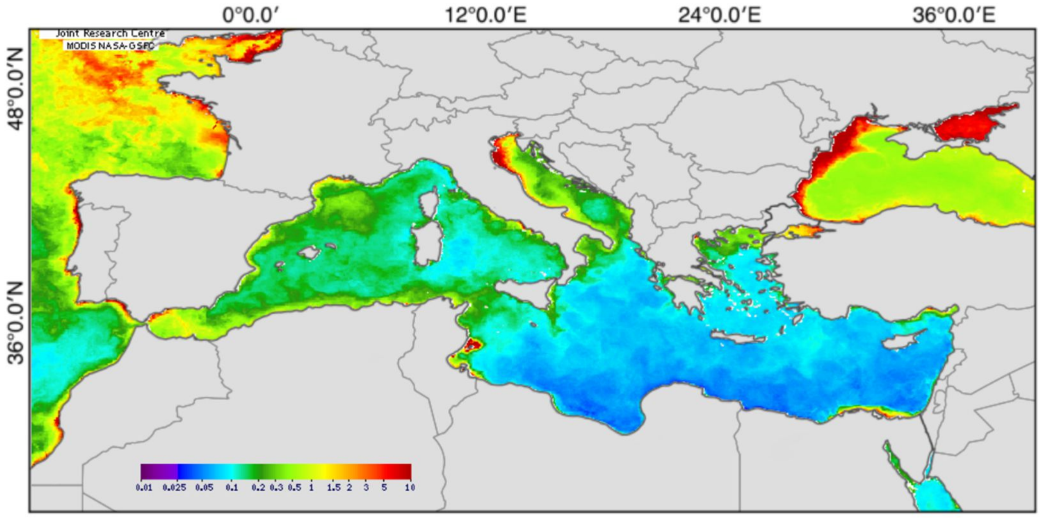

Figure 1.4 Surface chlorophyll-a concentration in the Mediterranean Sea in June 2009, used as a proxy of surface primary production, expressed as mg.m^{-3}. Data was retrieved from the Environmental Marine Information System (EMIS) (http://emis.jrc.ec.europa.eu/emis_1_0.php).

Overall water circulation

The Mediterranean thermohaline circulation is driven by the Atlantic Water (AW) which flows between 100-200 m eastward, becoming warmer and saltier (mean temperature: 14-15ºC; 36.5-38.3 psu) because of the air-sea interaction and mixing with the saltier Surface Mediterranean Water (Millot, 1999) (Fig. 1.5). In the northeastern Levantine basin, the Levantine Intermediate Water (LIW), a relatively dense and high-salinity water mass (15-16ºC and 39-39.2 psu) is formed due to winter cooling of the AW, and flows down to 600 m depth in an opposite direction through the basin (Millot and Taupier-Letage, 2005). LIW provides a preconditioning mechanism for the formation of the two locally formed deep water masses, the Eastern Mediterranean Deep Water (EMDW; 13.5ºC and 38.7 psu) and the Western Mediterranean Deep Water (WMDW; 12.7-12.9ºC and 38.4 psu) (Oddo et al., 2009).

Oceanographic mesoscale variability is complex and is responsible for sub-basin scale gyre structures (eddies), fronts and coastal upwelling that have implications for the primary productivity and the flux of organic matter to the seafloor (Pinardi et al., 2006; Danovaro et al., 2010; Tanhua et al., 2013) (Fig. 1.5).

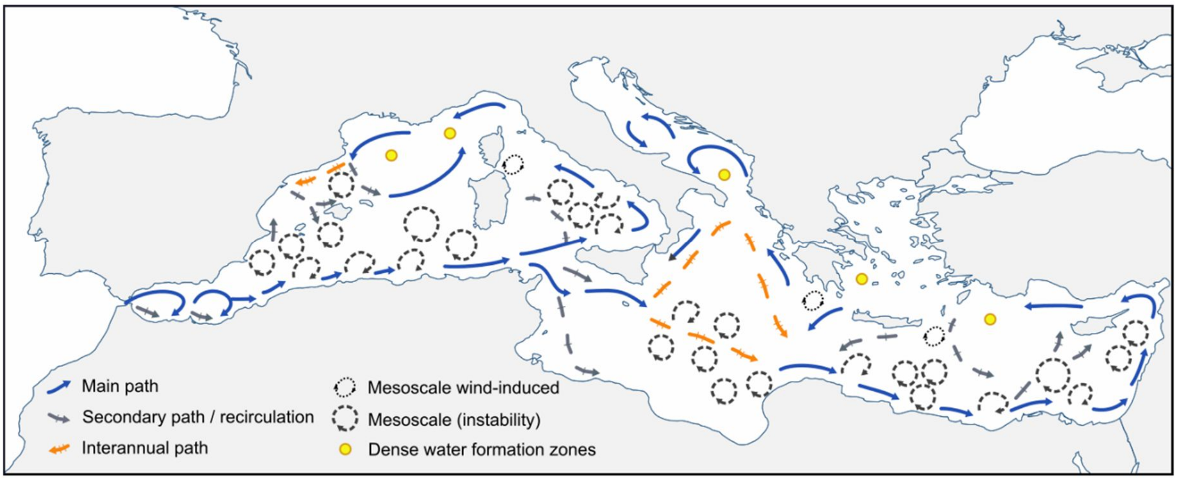

Figure 1.5 Overall water circulation driven by the Atlantic Water. Modified from Millot and Taupier-Letage (2005).

Oligotrophy

The Mediterranean Sea is oligotrophic, with decreasing productivity from west to east (Stambler, 2014). The western Mediterranean Sea (especially the Gulf of Lions) shows relatively high primary production values (140–160 mgC.m^{-2}.d^{-1}) and about 90% of this production is used before reaching the seafloor; in contrast, in the eastern Mediterranean Sea (and particularly the Cretan Sea), primary production estimates range between 19–60

$mgC.m^{-2}.d^{-1}$, and about 97–98% of the exported production is mineralised before reaching the sediments (Danovaro, 2003).

Phosphorus and nitrogen appear to be the most important limiting nutrients (Estrada, 1996; Stambler, 2014). These nutrients' deficiency may be related to the water exchange through the Gibraltar Strait where the Mediterranean Sea loses deep, relatively nutrient-rich water to the Atlantic Ocean and receives nutrient-poor Atlantic waters (Krom et al., 1991). Overall, this process results in lower organic matter concentrations in the Mediterranean than in other ocean regions (Tselepides et al., 2000a; Moran et al., 2002; Pusceddu et al., 2010a).

The oligotrophy together with high water temperature, which enhances the degradation of organic matter, results in a decrease in the quantity and quality of organic material with increasing depth and from west to east. Differences in flux rates between basins were shown by Danovaro (2003, comparing Barcelona canyon head vs. Cretan Sea slope), reporting mass fluxes up to 80 times higher and values of organic carbon, carbohydrates and proteins fluxes 1 to 2 orders of magnitude higher in the western than in the eastern Mediterranean Sea. In terms of quality of the nutrient inputs to the benthos (expressed as labile organic matter contribution to the total mass flux), 1–8% were estimated in the western Mediterranean basin in contrast to 0.8% estimated for the Cretan Sea. Because the Mediterranean deep-sea sediments become progressively impoverished in biochemical compounds (phytopigments, proteins, carbohydrates and lipids) and biopolymeric C from west to east, the productivity of the overlying water masses is a key factor controlling deep-sea benthic trophic conditions (Danovaro et al., 1999; Danovaro, 2003; Pusceddu et al., 2010a).

Besides primary productivity, other important processes control the export of biogenic particles from surface waters to the deep. These processes are subjected to spatial variability due to the sub-basin heterogeneity and localized topographic structures (e.g. canyons), but also to strong seasonal and inter-annual variability, caused by river runoff and atmospheric forcing (e.g. storms, winter deep convection), particularly relevant in the western basin (Estrada, 1996; Lopez-Fernandez et al., 2013b). Here, the inflow of Atlantic waters, and the resulting circulation patterns, are associated with nutrient enrichment in the southern zone e.g. turbulent mixing in the strait, which transport nutrients from the deep waters to the euphotic zone; upwelling, frontal zones and eddies which produce points of enhanced phytoplankton growth (Millot, 1999). Anthropogenic influence through terrestrial runoff is especially important in the northern zone, where several rivers (e.g.

Ebre, running into the Catalan Sea) and submarine canyons are important sources of nutrients to the deep (Estrada, 1996).

The northwestern Mediterranean Sea and the Catalan margin

A distinctive characteristic of the continental slopes of the northwestern (NW) Mediterranean Sea is the presence of numerous submarine canyons along the south and north Catalan margins and the western Gulf of Lion (main canyons: Foix, Blanes, La Fonera, Cap de Creus and Lacaze-Duthiers) (Fig. 1.6). In the last two decades several studies revealed the particular morpho-sedimentary conditions and highly variable hydro-sedimentary processes associated to short-term high-energy events such as coastal storms, dense shelf water cascading and offshore convection resulting in shifts in a variety of near-bottom physical variables (e.g. temperature, currents, mass fluxes) occurring at different spatial and temporal scales in this region (Canals et al., 2006; Canals et al., 2013; Lopez-Fernandez, 2013b). The same studies have defined these canyons as essential habitats i) with particular morpho-sedimentary conditions and highly variable hydro-sedimentary processes, acting as preferential conduits for particulate matter in the shelf waters, facilitating their descent to the deep basin (Canals et al., 2006), and ii) with particular conditions that are critical for life-cycle aspects such as reproduction and feeding, providing refuge for the resident fauna and favouring the development of biomass maxima for several fish and other species (Sardà et al., 2009; Ramirez-Llodra et al., 2010). Well-structured biological communities in the Mediterranean submarine canyons are characterized by low energy trophic webs clearly affected by anthropogenic pressures (Canals et al., 2013), namely fisheries (Puig et al., 2012; Pusceddu et al., 2014), litter accumulation (Ramirez-Llodra et al., 2013) and chemical pollution (Sanchez-Vidal et al., 2015).

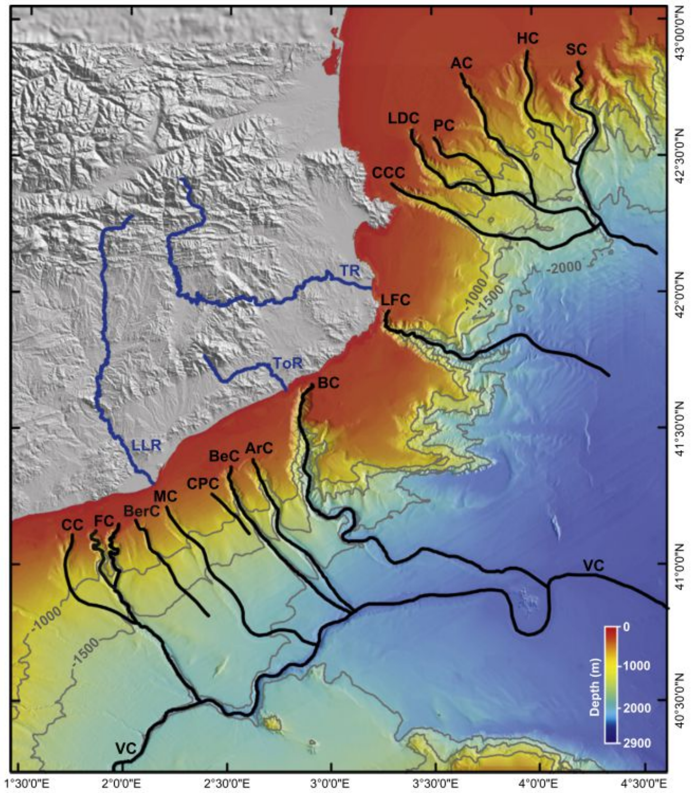

Figure 1.6 Submarine canyons of the western Gulf of Lion and the Catalan margin. Valencia Channel (VC) and main rivers opening at short distance from submarine canyon heads are also showed. HC: Herault Canyon. AC: Aude Canyon. PC: Pruvot Canyon. LDC: Lacaze-Duthiers Canyon. CCC: Cap de Creus Canyon. LFC: La Fonera Canyon. BC: Blanes Canyon. ArC: Arenys Canyon. BeC: Besos Canyon. CPC: Can Pallisso Canyon. MC: Morras Canyon. BerC: Berenguera Canyon. FC: Foix Canyon. CC: Cubelles Canyon. TR: Ter River. ToR: Tordera River. LLR: Llobregat River. From Canals et al., 2013.

In the NW Mediterranean Sea different aspects of primary production dynamics and the flux of particles are documented (Estrada, 1996 and references therein; Canals et al., 2013). Water-column stratification regularly occurs from April to November resulting in the formation of a chlorophyll maximum (DCM) in open waters (Estrada, 1996). A homogenized water column is present in winter and early spring with most downward flux occurring in the mixed layers. Plankton blooms typically occur in winter-spring, when surface waters start to stabilize, and in autumn, at the beginning of the mixing period (Margalef and Castellvi, 1967; Estrada, 1985). The spring bloom is more pronounced due to winter convection, which uplifts deep, nutrient rich waters to the photic zone subsequently triggering a pronounced phytoplankton bloom (Canals et al., 2013).

Advective processes such as discharges of continental run-off, episodic events caused by storms, dense shelf water cascading in the Gulf of Lion, offshore convection, eastern storms and the North Current may produce local food enrichment, channeled by submarine canyons (Canals et al., 2013). River floods, for example, represent a relevant food source, both quantitatively and qualitatively, to deep-sea marine ecosystems (Sanchez-Vidal et al., 2013). Adding to the typical vertical and lateral fluxes and sediment transport through slopes and canyon systems, these processes originate high spatial and temporal variability in biogeochemical composition and fluxes of particles to the deep Mediterranean seafloor. In particular, atmospheric forcing in this region is of utmost importance for the transfer of matter to the deep and overall functioning of the marine ecosystem. Canals et al. (2013) refer to the three relevant oceanographic processes as the ‘‘three tenors’’ of the NW Mediterranean basin (Fig. 1.7): dense shelf water cascading (DSWC, in late winter and early spring), eastern storms (in autumn and winter) and offshore convection (the later less relevant in terms of matter transfer to the deep).

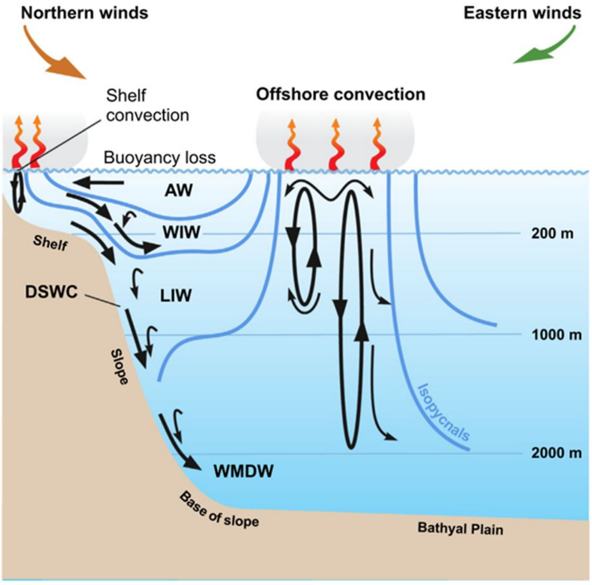

Figure 1.7 Scheme representing the three main oceanographic processes driving the NW Mediterranean Sea: dense shelf water cascading (DSWC), offshore convection and eastern storms (the ‘‘three tenors’’). The main water masses are also showed. AW: Atlantic Water; WIW: Western Mediterranean Intermediate Water; LIW: Levantine Intermediate Water; WMDW: Western Mediterranean deep water. From Canals et al., 2013.

DSWC is a near-bottom gravity current, where dense water originated on the continental shelf, by cooling and salinization, overflows the shelf edge down the continental slope until its density reaches the ambient density. It originates in the large shelf of the Gulf of Lion and, to a lesser extent, in the narrower North Catalan shelves of Roses and La Planassa (Durán et al., 2014), cascading downslope and mostly channeling through the submarine canyons (Canals et al., 2006; Durrieu De Madron et al., 2013). In years of intense cascading and/or offshore convection (e.g. 1998-1999, 2005-2006 and 2011-2012), these sinking surface waters form a turbulent, several tens of meters thick flow loaded with sedimentary particles that are able to erode the seafloor (Canals et al., 2006; Durrieu De Madron et al., 2013). The main conduits in carrying dense shelf waters downslope are, by order the canyons of Cap de Creus, La Fonera, Blanes and Lacaze-Duthiers. Cascading episodes usually start in late winter and extend till mid spring, thus overlapping with the annual spring phytoplankton bloom.

Open-ocean convection is the result of durable and local vertical mixing reaching the mesopelagic or bathypelagic layers (at depths greater than 2000 m). It also occurs at late winter and early spring, more or less synchronized with cascading (Stabholz et al., 2013). One major difference from dense shelf water cascading is that waters involved in offshore convection are loaded mostly with fresh organic matter and not with sediments.

Eastern storms in the NW Mediterranean Sea are an oceanographic response to cyclogenesis leading to the generation of eastern winds that become charged with moisture while blowing over the sea surface (Canals et al., 2013). Sanchez-Vidal et al. (2012) illustrated the power of eastern storms during a major event that occurred on the 26th of December 2008 and lead to the remobilization of a shallow-water reservoir of marine organic carbon associated with fine particles, resulting in its redistribution across the deep basin down to at least 1500 m deep.

The transport of particles during and after these events is not near-bottom restricted; instead it results in the formation of a long-lasting benthic nepheloid layer, with a height range of 200–500 m above the seafloor, which covers the entire western Mediterranean deep basin (Puig et al., 2013).

These processes occurring mainly during winter and spring contrast with low fluxes of particles in summer months when vertical hemipelagic settling prevails under quiescent atmospheric and oceanographic conditions (Canals et al., 2006, Pusceddu et al., 2010b; Canals et al., 2013). During summer, sporadic increases in particle fluxes occur due to atmospheric dust inputs (Lopez-Fernandez et al., 2013b). Other source of particle fluxes is associated to short-lived episodes of high turbidity and current speed caused by bottom trawl-induced sediment gravity flows (Puig et al., 2012). Such anthropogenic contributions to particle fluxes are best detected under calm conditions (usually during summer), when they do not overlap with naturally higher fluxes (like in autumn, winter and early spring months) (Canals et al., 2013). The highly dynamic processes acting in the NW Mediterranean Sea support deep-sea ecosystems with inputs of particles mostly by advection and from the photic zone, both lithogenic and highly-nutritive fresh organic material (Sanchez-Vidal et al., 2009; Lopez-Fernandez et al., 2013a; Pasqual et al., 2013). This represents an intermittent but highly relevant food resource for the deep margin and basin ecosystems (Canals et al., 2013). Particle fluxes loaded with organic matter are crucial to sustain deep-sea benthic and pelagic life, especially in oligotrophic systems such as the Mediterranean Sea, and may be responsible for a patchy distribution of biological assemblages (Canals et al., 2013).

1.1.3.2 Deep-sea Mediterranean fauna

The fauna of the deep Mediterranean Sea displays a number of particular characteristics: i) it consists mainly of eurybathic species - at depth greater than 500 m the fauna comprises six times more species in common with the upper layers than strictly deep-water species (Peres, 1987); ii) there are few representatives of typical bathyal or abyssal taxonomic groups - this is particularly evident in the western basin, where maximum depth is not exceeding 3000 m although in the eastern Mediterranean, abyssal species may be dominant (e.g. Matapan Trench, 5050 m, Laubier and Emig, 1993) iii) some faunal groups such as macroscopic foraminiferans, echinoderms, glass sponges and tunicates are scarce or absent (Danovaro et al., 2010) iv) the cold water stenothermal species, that represent the major part of the deep-sea fauna, are unknown in the Mediterranean Sea (Emig, 1997) iv) the endemicity of the deep-sea Mediterranean fauna decreases with increasing depth so that deep-water endemic species are few and generic endemism at genus-level is truly exceptional (Fredj and Laubier, 1985; Bellan-Santini et al., 1992). Briggs (2007) suggested that the fauna of the Mediterranean Sea (including invertebrates and fishes) is more diverse than the one from the Atlantic and displays considerable endemism. The Mediterranean coast is recognized as holding one of the most diverse faunas on the planet, but the same might not hold true for the deep-sea Mediterranean (Coll et al., 2010). Recent estimates of the overall deep-sea Mediterranean biodiversity account for approximately 2805 species, of which 66% are still undiscovered, with an important fraction of megafauna and macrofauna species remaining unknown (Danovaro et al., 2010).

The Mediterranean deep-sea fauna is relatively recent when compared to the Atlantic one and it is also less diverse and abundant. Apparently these conditions are more severe in the eastern Mediterranean (Bouchet and Taviani, 1992). Two main reasons explain the peculiarities of this fauna:

i) Geological history: the most important geological event, the Messinian crisis at approximately 5.96 million years ago, consisted in the near drying out of the Mediterranean basins and subsequent isolation from the Atlantic Ocean when the water mass exchanges through the Gibraltar Strait were interrupted. These events resulted in a massive decrease of most phyla's representatives, especially the ones from deeper waters (Emig and Geistdoerfer, 2004). After this event, the Mediterranean Sea was colonized by relatively shallow Atlantic fauna that apparently evolved without major changes, except for the Quaternary climate oscillations (e.g. anoxic events) and subsequent faunal replacements (Fredj and Laubier, 1985).

ii) Oceanography: faunal exchange with the Atlantic Ocean is impaired by differences in temperatures (differences of up to 10ºC between the Atlantic Ocean and the Mediterranean Sea at the same depth) which difficult the colonization by Atlantic fauna; other barriers also difficult the colonization such as the shallow straits, salinity and oligotrophy (Peres, 1987; Emig and Geistdoerfer, 2004). Nevertheless, there are locally habitats with relatively high benthic abundances, such as in the vicinity of submarine canyons (Canals et al., 2006), and in abyssal trenches (Tselepides and Lampadariou, 2004).

Bouchet and Taviani (1992) have further hypothesized that high near-seafloor temperatures and salinities have led to a Mediterranean deep-sea fauna that consists of reproductively sterile pseudopopulations entering the Mediterranean Sea as meroplankton through the Atlantic inflow at Gibraltar. However, it has been demonstrated that the populations of the most common benthic molluscs at depths greater than 1000 m in the Levantine Sea are composed of both adult and juvenile specimens. In fact, the most common and abundant species in the eastern Mediterranean Sea, *Yoldia micrometrica*, was never recorded at the westernmost regions. Moreover, brooding benthic decapod crustaceans and fish have been collected repeatedly from the depths of the Levantine Sea (Galil and Goren, 1995; Goren and Galil, 1997). Though much reduced in species richness when compared to the western and central Mediterranean deep-sea fauna, the

Levantine bathyal benthos is composed of autochthonous, self-sustaining populations of opportunistic, eurybathic species that have colonised the region following the last sapropelic event (Galil, 2004). For strictly deep-sea macrobenthic species (e.g. the decapod crustacean family Polychelidae), the Gibraltar Strait is not an impenetrable barrier (Abelló and Cartes, 1992).

Drivers for the deep-sea Mediterranean biodiversity patterns

Studies on the Mediterranean deep-sea benthic fauna have increased in the last decades and there is progress towards a more comprehensive view of the patterns and drivers of deep-sea biodiversity in this peculiar basin (Danovaro et al., 2010). Since the late 1980s, several projects were designed for systematic investigation of depths greater than 1000 m and several deep-sea benthic studies have been conducted in the Mediterranean Sea targeting megafauna, meiofauna and, to a lesser extent, macrofauna and prokaryotes (Danovaro et al., 2010 and references there in).

It has been proposed that benthic biodiversity patterns in the deep Mediterranean are driven by the West-East oligotrophic gradient. However, a recent review (Danovaro et al., 2010) showed that these patterns are not consistent for all benthic groups and other factors are indicated to influence biodiversity. Basin-specific environmental drivers, which include seasonal changes in surface primary production and food availability to the seafloor, mesoscale temporal variability on oceanographic processes (storms; discharges of continental runoff; thermocline) and topographic differences (e.g. canyons) support different benthic assemblages (Tselepides et al., 2004; Danovaro et al., 2010; Tecchio et al., 2011b). Also, it should be considered that the West-East differences in the deep-sea Mediterranean biodiversity could be related to a different evolutionary history, related to the Messinian crisis (Danovaro et al., 2010). Temporal trends are less studied than spatial ones especially in areas were both vertical and lateral fluxes of organic matter are relevant. Few studies revealed that abundance, biomass and biodiversity in the Mediterranean deep-sea fauna might be driven by temporal variability in both food availability and quality and/or in response to high energetic events (Gambi and Danovaro, 2006; Company et al., 2008; Mamouridis et al., 2011; Pusceddu et al., 2013).

Research indicates a variety of patterns among different benthic groups. Regarding the epibenthic megafauna, bony fishes and decapods crustaceans are the main groups represented in the deep Mediterranean fauna. Non-crustacean invertebrates are less common (Ramirez-Llodra et al., 2008; Tecchio et al., 2011b), in contrast to the Atlantic Ocean where some groups such as echinoderms are dominant (Billett, 1991). The epibenthic megafaunal communities of the Mediterranean continental margins are known to show a strong bathymetric zonation which has been associated to hydrological characteristics, food availability, sediment type and changes in the steepness of slope; a peak of biomass occurs at around 1200 m depth, followed by a reduction in abundance, biomass, body size and diversity at depths greater than 1500 m (Cartes and Sardà, 1993; Stefanescu et al., 1994; Company et al., 2004; D´Onghia et al., 2004; Tecchio et al., 2011a). Studies at a larger spatial scale showed a decrease of abundance and biomass from West to East, along the oligotrophy gradient, and the lowest biodiversity in the more oligotrophic eastern region (Company et al., 2004; Sardà et al., 2004; Tecchio et al., 2011b).

Most studies concerning bathyal macro-infauna of the Mediterranean basin provide qualitative information (e.g. Fredj and Laubier, 1985); quantitative data is very limited and insufficient to accurately describe the composition and structure of these communities in this region. In the western basin, to our knowledge, the limited number of studies were performed in slope and canyon areas. Mamouridis et al. (2011) suggested an increase in the macro-infauna abundance and biomass, mostly represented by polychaetes, in areas of high food availability, such as the ones found in the Bèsos Canyon, while adjacent areas were dominated by bivalves and sipunculids. In the Toulous Canyon a bathymetric decrease in biomass, density and diversity of macrofauna, with a major species turnover at 1000 m, was observed. This was explained by a corresponding change in the sediment composition which is often considered a major driver for the distribution of macrofaunal species (Stora et al., 1999). Down to 1000 m depth particle transport is dominated by lateral advection of the benthic nepheloid layer while at greater depths it is dominated by downflux from the water column (Stora et al., 1999).

In the Cretan sea (eastern basin), bathyal infauna characterized mostly by polychaete species, also presented a sharp bathymetric decrease in abundance, biomass and diversity, but with major species turnover at 200, 500 and 1000 m - this pattern is likely strongly related to corresponding decreases in food availability (Tselepides and Eleffheriou, 1992; Tselepides et al., 2000a). Significant correlations between bathyal macro- and meiofauna and sediment variables (especially the ones indicating food availability) led to the conclusion that food availability is the major limiting factor in the system (Tselepides and Eleffheriou, 1992; Danovaro et al., 1999; Tselepides et al., 2000b; Tselepides and Lampadariou, 2004).

Suprabenthos, the vagile component of benthos (described in detail in the next section) is subjected to gradients similar to those affecting benthos (Cartes et al., 2011). Several studies provided valuable quantitative information regarding the composition and structure of the bathyal suprabenthos in the western basin. These studies revealed that the abundances and/or biomasses were higher at intermediate depths (approx. 800-1200 m, D'Onghia et al., 2004) or in localized food enriched environments, such as canyons, while changes in assemblage composition were mainly related to depth (Catalan Sea: Cartes and Sorbe, 1993; 1995, 1997, 1999a; Cartes, 1998; Cartes et al., 2003) and season, although the latter was less evident (Balearic islands: Cartes et al., 2008, 2011). Changes in suprabenthic diversity appear to be related to the frequency and intensity of disturbance regimes mediated by oceanographic processes (Cartes et al., 2011) with the consequent changes in the sediment properties.

Considerable work has been carried out on meiofauna (and particular on nematodes) (Danovaro et al., 2010; Gambi et al., 2010 and references therein). Typically, the abundances decrease with increasing depth and from west to east (Danovaro et al., 1999, 2008b) except in submarine canyons and trenches, where high abundances were reported due to favourable trophic conditions (Tselepides and Lampadariou, 2004; Bianchelli et al., 2013). The results of different studies are somehow inconsistent in relation to the reported diversity patterns: a lack of unimodal or exponential pattern (Danovaro et al., 2009a; 2010); a decreasing bathymetric trend (Danovaro et al., 2008b; Sevastou et al., 2013); a hump-shaped pattern (Danovaro et al., 2010). At a wide-basin scale, a decreasing longitudinal gradient in diversity is reported for nematodes and attributed to the decrease in quantity and bioavailability of trophic resources, in a west-to-east direction (e.g. Danovaro et al., 1999, 2008b, Bianchelli et al., 2013) and also from north to south in the Aegean Sea, supporting the hypothesis of a link between diversity and productivity (Lampadariou and Tselepides, 2006). However, other studies showed no such link (Danovaro et al., 2008b). High β-diversity, in relation to depth and longitude (Danovaro et al., 2008b, 2010, Bianchelli et al., 2013), can be considered as a rule in the deep-sea sediments of the Mediterranean Sea. Bianchelli et al. (2013) ranked β-diversity as more important than α-diversity for understanding the relation of diversity patterns and their drivers in the deep Mediterranean Sea.

Microbial benthic community studies have been performed recently in the deep Mediterranean Sea. The limited available information reports high and unique benthic prokaryotes diversity, with high levels of turnover diversity between the western, central, and the eastern Mediterranean Sea, and bacterial richness comparable to other deep-sea regions (Bowman and McCuaig, 2003; Polymenakou et al., 2005). In the study by Luna et al. (2004) bacterial biodiversity parameters did not display any relationship with water depth.

In conclusion, an overall decrease in abundance, biomass and species richness has been observed from northwestern to southeastern areas and with depth for several benthic compartments, related to the decreasing of food availability to the seafloor when moving eastwards and with increasing depth (Danovaro et al., 1999). However, the same could not hold true for the benthic biodiversity. A recent study performed by Danovaro et al. (2010) suggested that the longitudinal trend in biodiversity is apparently weak and the effects of food supply (i.e. energy availability) may be important for certain components but can be shaped by other factors that influence deep-sea diversity.

Trophic structure in the Mediterranean deep-sea fauna

There is a growing interest in investigating the diversity of organism traits or functional diversity because the functions performed by taxa determine ecosystem properties and processes. Within the Mediterranean Sea, differences in the trophic webs are related to differences in the energy input. Fish assemblages in the eastern basin are sustained by mesopelagic food sources (Madurell and Cartes, 2005), given the extreme oligotrophic conditions; in the western basin, benthic assemblages on continental margins and under the influence of submarine canyons are mainly sustained by benthic food sources (Cartes and Maynou, 1998), in contrast to insular areas were assemblages are mainly sustained by pelagic food sources due to the lack of advective processes of food input (Cartes et al., 2001; Fanelli et al., 2013).

Major changes in the macrobenthic trophic structure composition are found along the West-East oligotrophic gradient, with a higher contribution of carnivores/scavengers and filter feeders in the eastern basin, because of food limitation but also due to specific hydrodynamic conditions (Baldrighi et al., 2014). In submarine canyons, macrofaunal assemblages are mostly dominated by surface-deposit feeding polychaetes and crustaceans and opportunistic species in response to periods of high food availability and variability in food sources, while subsurface deposit feeders are dominant over the adjacent slope (Mamouridis et al., 2011). Also, anthropogenic pressure due to trawling fisheries in the upper canyons (and their consequences in food availability) change the trophic structure of the assemblages, by a reduction of mega-epibenthic and endobenthic deposit feeders and increase in scavengers (Ramirez-Llodra et al., 2009). Changes in food availability along a bathymetric gradient also modifies the trophic structure. For example, predator abundances are known to increase with depth due to the decrease in availability of food sources, as observed for the macrofauna in the eastern Mediterranean (Tselepides et al., 2000a).

Besides depth, vertical distribution of food in the sediment or in the vicinity of the seafloor is a main structuring factor of benthic assemblages. The exploitation of different food sources near the seafloor results in a gradual decrease in the dependence of suspended matter and an increase in the exploitation of suspended matter from sediment, from zooplankton to benthos, with suprabenthos exploiting both resources (Cartes al., 2008; Fanelli et al., 2009b; Mamouridis et al., 2011).

1.1.4 Suprabenthos

The benthic boundary layer (BBL) is defined as the layer of water adjacent to the seafloor which can be extended from a few cm to tens of meters, depending both temporally and spatially on various physical and biogeochemical processes (Marshall and Merret, 1977). It is usually limited to the immediate vicinity of the seafloor at shallow depths (continental shelf) while in the deep-sea it is usually extended to tens of meters. It is characterized by high complexity because it is the interface between pelagic and benthic environments, communities and processes: i) usually higher concentrations of particles and biomass are found in comparison to the water layer above it (Boudreau and Jorgensen, 2001); ii) it plays an important role in the exchange of particles (resulting from vertical and lateral processes) between the sediment and the water column and iii) shelter a diversified fauna from the pelagic and benthic realms consisting of a variety of ecological groups (e.g. benthic, benthopelagic, nektonic, planktonic) (Gage and Tyler, 1991; Vereshchaka, 1995).

The mobile macrofauna occupying the immediate water layer adjacent to the seafloor has received different terminologies and theoretical composition according to different authors, often associated to the region or taxa studied (Mees and Jones, 1997). The term hyperbenthos, introduced by Beyer (1958), was later defined as the association of animals living in the water layer close to the seafloor (Mees and Jones, 1997) and includes typical species, planktonic species derived from their downward extensions and endo- or epibenthic species as they emerge into the water column. Brunel et al. (1978) defined this fauna as suprabenthos, the bottom dependent animals, mainly crustaceans, which perform - with varying amplitude, intensity and regularity - seasonal or daily vertical migrations above the seafloor. These terms are used in northern temperate areas, in shallow areas (e.g. estuaries, Dauvin et al.,2013) and in the deep-sea (e.g. Cartes, 1998, Mediterranean Sea; Frutos and Sorbe, 2014; Bay of Biscay).

Dauvin and Vallet (2006) classified the near-bottom layer fauna in different groups according to their swimming capacity and bottom dependence: (i) permanent (e.g. copepods, chaetognaths, euphausiids) and temporary (e.g. crustacean and fish larvae) swimmers present only in the BBL or throughout the water column, which are also considered as zooplankton; (ii) burrowers/swimmers, which correspond to suprabenthos (Brunel et al., 1978) (iii) burrowers and temporary nuptial swimmers emerging during the nuptial period (e.g. polychaete syllids and nereids) as well as benthic mobile and drift species (e.g. bivalves and polychaetes), most of which are epibenthic, and (iv) fish.

Vereshchaka (1995) studying the near-bottom macroplankton/benthopelagic composition in slopes and seamounts defined three ecological groups among benthopelagic organisms: i) hypobenthopelagic animals, which spend part of their life in the benthopelagic layer and the rest further below, in the benthic biotope; they correspond to the suprabenthos (e.g. mysids, shrimps and cumaceans) described by Brunel et al. (1978); ii) epibenthopelagic animals, which spend part of their life in the benthopelagic layer and the rest further above, in the pelagic biotope (e.g. zooplankton) iii) amphibenthopelagic animals, which periodically live in all three biotopes – pelagic, benthopelagic and benthic.

Other terminologies have been used for the same fauna. For example, demersal zooplankton is used in tropical areas and bathypelagic plankton designate the same fauna in the deep-sea and the zone occupied as BBL (Mees and Jones, 1997). From the above examples, there is little mutual acknowledgment to designate the macrofauna occupying the water layer adjacent to the seafloor, partly attributed to the broad diverse forms related to distribution in space and not to phylogeny or functionality (Mees and Jones, 1997).

In this Thesis the term suprabenthos is adopted because it is the term that, in my opinion, better describes the fauna targeted by the Macer-Giroq suprabenthic sledge. Also, previous works in the Mediterranean have used the term suprabenthos. Moreover, this Thesis concerns only the crustacean assemblages.

Suprabenthos is a complex compartment mainly composed of peracarids (e.g. mysids, amphipods) and other crustacean taxa (e.g. euphausiids, natantian decapods).

The main biological feature of peracarids is the direct development of embryos in brood pouches (oostegites) of adult females, while euphausiids and decapods have typically free planktotrophic larvae that aggregate in the photic zone (Cartes et al., 2010).

Despite the sparse knowledge on suprabenthic communities, the relevance of this fauna in marine food webs has been emphasized by several authors. In the western Mediterranean basin, deep-sea dietary studies concluded that suprabenthos (e.g. amphipods, mysids) is an important food source for higher trophic levels (Cartes, 1994; Carrassón and Cartes, 2002; Cartes et al., 2008). Many of the suprabenthos predators are of high commercial value, such as the hake *Merluccius merluccius* (Bozzano et al., 1997) and the red shrimp *Aristeus antennatus*, an important target species of Mediterranean deep-sea fisheries (Sardà et al., 2009). Suprabenthos is particularly important in the diet of decapod juveniles and small myctophids that consume specific preys (Cartes et al., 2004).

Isotopic signature studies revealed that suprabenthic crustaceans occupy 2-3 trophic levels as they exploit a large diversity of food sources, mobilizing organic and detritus particles and their associated microbes from the sediment and water column, or preying on meiobenthos and zooplankton (Madurell et al., 2008; Fanelli et al., 2009a, 2009b). The swimming behaviour and diel vertical migrations performed by some suprabenthic groups (e.g. euphausiids, hyperiids) or species may contribute to the carbon recycling in the water column and their export to the deep benthic ecosystems (Dilling and Alldredge, 2000; Trueman et al., 2014). However, most studies on bathyal suprabenthic assemblages reported limited migrations for few species or even no nocturnal migrations (Cartes and Sorbe, 1995; Cartes, 1998, Cartes et al., 2011; Koulouri et al., 2013; Frutos and Sorbe, 2014).

The burrowing behaviour of some suprabenthic species at the water-sediment interface can also contribute to the biogenic modification of the sediment (bioturbation, bioresuspension), and increased particle flux (Brandt, 1993; Graf and Rosenberg, 1997). Suprabenthos is characterized by high productivity/biomass ratios (Cartes and Sorbe, 1999b; Cartes et al., 2002). In fact, Cartes and Maynou (1998) suggested that suprabenthos is responsible for *ca.* 50% of the benthic production. Nevertheless, and despite its ecological importance, the biodiversity of suprabenthos has rarely been considered in benthic-pelagic coupling and energy fluxes studies (e.g. development of models) (Tecchio et al., 2013).

1.2 Objectives and Thesis outline

The continental slopes are primary sites for marine biodiversity research since they are subjected to a wide range of environmental gradients with complex relationships between the environment and biodiversity at different scales. Continental slopes of the Mediterranean Sea are warm-water isothermic and longitudinally trophic-graded, making them a relevant study area to test for patterns of species distribution and biodiversity. A distinctive characteristic of the continental slopes of the western Mediterranean Sea is the presence of submarine canyons which are thought to play an important role in the funnelling of nutrients to the deep basin in this oligotrophic system (Canals et al., 2013). Moreover, owing to their proximity to highly populated coastal areas, Mediterranean submarine canyons are subjected to several threats, such as pollution and fisheries, making them of particular interest to be studied.

Despite its ecological importance, the suprabenthos is globally a less studied benthic component, particularly in the deep sea. The evidence of their role in the deep-sea food webs and ecosystem functioning requires more knowledge on suprabenthic species distribution and biodiversity.

Recognizing the importance of deep-sea and suprabenthos research, this Thesis intends to contribute to the knowledge of the drivers of suprabenthic assemblages inhabiting the slopes of bathyal Mediterranean Sea, specifically: i) along a longitudinal gradient of increasing oligotrophy from west to east ii) in a submarine canyon and adjacent slope iii) and in relation to varying environmental conditions at different spatial and temporal scales.

The main results are organized in five chapters:

- Chapter 2.1 describes the sampling procedure and characterizes the overall studied suprabenthic assemblages; it provides an overview on the biological sampling and a list of species for the region together with their bathymetric distributions.
- Chapters 2.2 and 2.3 are focused on the drivers along large-scale gradients; the results on suprabenthic biodiversity and trophic structure in two Mediterranean regions are presented in Chapter 2.2; Chapter 2.3 further elaborates the suprabenthic near-bottom vertical distribution, biodiversity and trophic structure along a large longitudinal and bathymetric gradient and in relation to trophic variables.

- Chapters 2.4 and 2.5 are focused on a regional scale; the results on biodiversity and trophic structure along a submarine canyon and adjacent open slope subjected to seasonal variability in hydrodynamic processes and trawling pressure are presented in Chapter 2.4 while Chapter 2.5 explores the suprabenthos assemblages in relation to the inter-annual variability in oceanographic processes and energy driven events. This Thesis is finalized with brief remarks on current knowledge of suprabenhic assemblages and main conclusions.

The chapters 2.2, 2.3, 2.4 and 2.5 of this Thesis are presented as research articles and are either published, submitted or being prepared for submission (listed below). Consequently, there is inevitably some degree of overlap among the different chapters, particularly in the introduction and material and methods sections.

Almeida, M., Plaiti, W, Tselepsides A., Sardà F., Cunha, M.R. (in preparation). Deep-sea crustacean suprabenthic community structure and biodiversity in the western and central Mediterranean Sea. To be submitted to Deep-Sea Research I. (Chapter 2.2)

Almeida, M., Frutos, I., Tecchio, S., Lampadariou, N., Company, J.B., Ramirez-Llodra, E., Cunha, M.R. (published online 2017). Biodiversity patterns of crustacean suprabenthic assemblages along an oligotrophic gradient in the bathyal Mediterranean Sea. Deep-Sea Research I. (Chapter 2.3)

Almeida, M., Frutos, I., Company, J.B., Martin, D., Cunha, M.R. (published online 2016). Biodiversity of suprabenthic peracarid assemblages from the Blanes Canyon region (NW Mediterranean Sea) in relation to natural disturbance and trawling pressure. Deep-Sea Research II. (Chapter 2.4)

Almeida, M., Tecchio, S., Cunha, M.R, Company, J.B. (in preparation). Suprabenthic crustacean assemblages subjected to high-energy hydrodynamic events in the Blanes Canyon and adjacent slope (NW Mediterranean Sea). To be submitted to Journal of Sea Research. (Chapter 2.5)

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SECTION 2. RESULTS

2.1 Characterization of suprabenthic assemblages from the bathyal Mediterranean Sea

2.1.1 Introduction

The Benthic Boundary layer (BBL) is the layer of water adjacent to the seafloor (extends a few tens of meters into the water column) with high complexity because it is the interface between the pelagic and the benthic environments. The BBL shelters a diversified fauna from the pelagic and benthic realms consisting of a variety of ecological groups classified according to their swimming capacity and bottom dependence (e.g. Vereshchaka, 1995; Dauvin et al., 2006). Suprabenthos, an important component of the BBL macrofauna, includes the swimming bottom dependent animals (mainly peracarids) with migratory behavior (Brunel et al., 1978; Koulouri et al., 2013), and other groups periodically associated with the substrate (Cartes et al., 2008; Koulouri et al., 2009). This fauna has received different terminologies (e.g. hyperbenthos, BBL macrofauna, demersal zooplankton or benthopelagic plankton) and therefore there is little mutual acknowledgment in the definition and composition of suprabenthos (Mees and Jones, 1997). The ecological role of these organisms has been highlighted by several authors. They form a link between the benthic and the pelagic environment because of their daily migrations (e.g. Brandt, 1993); their motility also contributes to the resuspension and biodeposition (e.g. Dilling and Alldredge, 2000). Most groups are an important food source for fishes and decapods and others feed on meiofauna, while some groups feeding on detritus, are important for the remineralization of refractory material (e.g. Carrassón and Cartes, 2002; Fanelli et al., 2009).

The difficulty of sampling the motile and uneven distributed animals dwelling close to the seafloor with benthic (e.g. grabs, corers) or planktonic samplers (e.g. plankton nets) led to the development of gears that sample the suprabenthic macrofauna at various distances from the bottom (e.g. Hesthagen, 1973; Rothlisberg and Pearcy, 1977; Sorbe, 1983; Dauvin and Lorgere, 1989; Cartes et al., 1994; Brandt and Barthel, 1995; Koulouri et al., 2003) (Fig. 2.1.1). Generally, these are equipped with small mesh-size nets mounted in a sledge at different levels above the seafloor and towed at an adequate speed (1–2 knots). The sledges are also often equipped with an opening-closing system to avoid contamination, an odometer for measuring the towed distance and a flowmeter to measure the water filtered (Mees and Jones, 1997). Most of these gears sample at least >10 cm above the seafloor to avoid contamination from the sediment and the organisms living on the top of or in it. To minimize this problem, improved techniques have been applied by combining additional sampling (grab or corer) which allows apportioning the organisms to the appropriate biota (Eleftheriou, 2013). Other authors designed a sampling gear equipped with an artificial resuspension system to collect the fauna at the first centimetres above the seafloor (Koulouri et al., 2003). This gear was also used to study the impact of bottom trawling on this fauna, a huge concern in the Mediterranean Sea (Ramirez-Llodra et al., 2011). In some cases, a video camera is positioned at the gear in order to provide visual information on the sampling performance, bottom topography and megafaunal densities (Brandt et al., 2013).

Figure 2.1.1 Examples of gears used to sample the epibenthic/suprabenthic macrofauna. A: Modified Sanders sledge (Mastrototaro et al., 2010); B: Sorbe sledge (http://www.theseusproject.eu/wiki/Sampling_tools_for_the_marine_environment); C: TTS sledge (Koulouri et al., 2003); D: EBS sledge (http://www.oceanblogs.org/so237/2014/12/22/); E: Brenke sledge (http://abyssline.blogspot.pt/2015/03/thats-one-giant-sled-brenke-sledge.html); F: Macer-Giroq sledge (Dauvin et al., 1995).

Despite the recurrent improvements in the sampling gears, the suprabenthic fauna from different marine environments remains poorly studied (Mees and Jones, 1997). One of the reasons is that suprabenthic studies are still limited by technical difficulties in sampling efficiently the water layer just above the seafloor where most of suprabenthic organisms are concentrated (Mees and Jones, 1997; Koulouri, 2014). In the deep North Atlantic Ocean, most studies are confined to the northeast margin around Europe (e.g. Elizalde et al., 1991, 1993; Dauvin et al., 1995; Cunha et al., 1997; Marquiegui and Sorbe, 1999; Dewicke, 2002; Vanquickelberghe, 2005; Sorbe and Elizalde, 2014). Some studies were also conducted in polar areas (e.g. Arctic Ocean: Sirenko et al., 1996; Brandt, 1997; Brandt and Brenke, 2007; Antartic Ocean: San Vicente et al., 2007, 2009; Lorz and Brandt, 2003; Lörz et al., 2013), in the South Atlantic Ocean (Angola Basin: Brandt, 2005; South Polar front: Brandt, 2014;) and in the northwest Pacific (Sea of Japan: Brandt et al., 2013; Kuril–Kamchatka Trench: Brandt and Malyutina, 2015). In the Mediterranean margins, information on the distribution of deep-sea suprabenthos is mostly confined to the upper slopes of the western Mediterranean Sea (e.g. Cartes and Sorbe, 1993; Cartes et al., 2003, 2011). In the central Mediterranean Sea, to our knowledge, information on suprabenthos is lacking, and for the eastern region only few studies have been conducted including particular taxa or the whole assemblage at shallow depths (Hatzakis, 1982; Stefanidou and Voultsiadu-Koukoura, 1995; Sorbe et al., 2002; Sorbe and Galil, 2002; Madurell and Cartes, 2003; Koulouri et al., 2013).

In this chapter we provide an overview on the suprabenthic sampling carried out under the scope of RECS, PROMETEO, DOSMARES, BIOFUN and DESEAS projects, recovered from mud sediments of the bathyal Mediterranean habitats, in open slopes and in a submarine canyon, from approximately 450 to 3000 m. The results obtained during these studies are explored in detail in chapters 2.2 to 2.5 but the aim of this chapter is to provide an easy-access check-list compiling the data on the species collected during these projects in order to extend the spatial and bathymetric coverage of the knowledge on the composition and community structure of the bathyal Mediterranean Sea suprabenthos in canyon and open slope habitats.

2.1.2 Material and methods

2.1.2.1 Study area

Sampling was carried out across the Mediterranean Sea and included the following regions of the continental slope: Blanes canyon and adjacent slope (Catalan Sea), and the South Balearic Sea in the western basin, the Ionian Sea in the central basin, and the south of Crete in the eastern basin. The samples covered the depth range between 450 to 3000 m (Fig. 2.1.2) and were carried out between 2001 and 2012. Information of the projects and cruises is presented in Table 2.1.1.

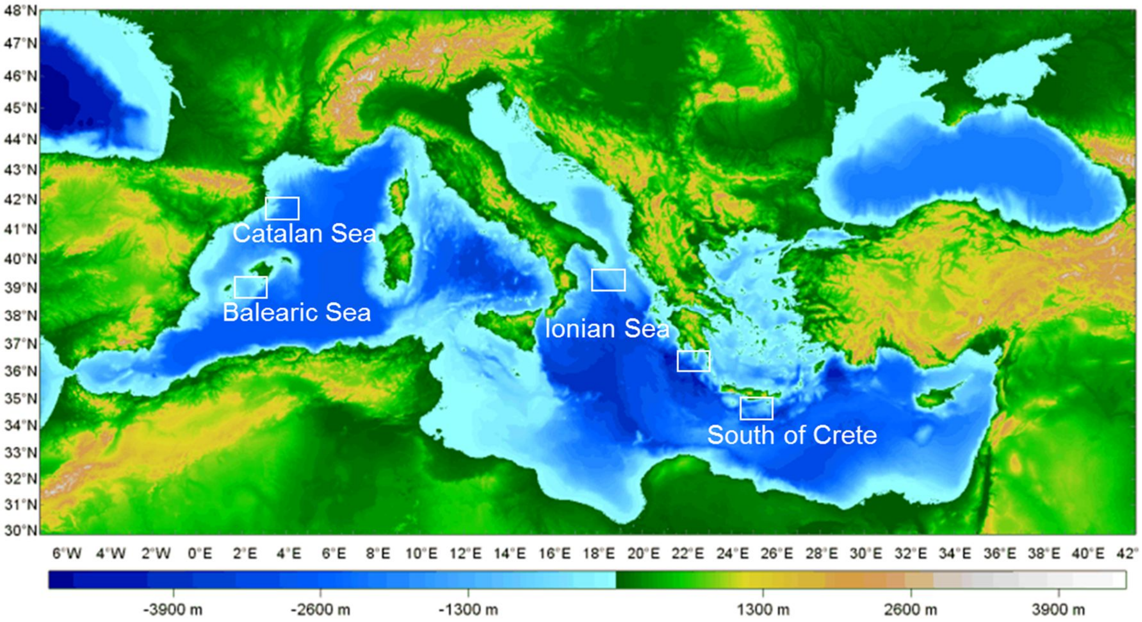

Figure 2.1.2 Map of the sampling sites. Catalan Sea and Balearic Sea in the western Mediterranean Sea (W), the western and eastern Ionian Sea in the central Mediterranean Sea (C) and South of Crete in the eastern Mediterranean Sea (E) (http://www.unipv.it/cibra/MedBathy%20800.gif).

Two trans-Mediterranean cruises, DESEAS cruise performed in June-July 2001, sampled the southern Balearic Sea and the eastern Ionian Sea at 600 m, 1000 m and 2000 m depth and the BIOFUN cruise performed in May-June 2009, sampled the southern Balearic Sea, western Ionian Sea and south of Crete at 1200 m, 2000 m and 3000 m depth. These sites are located in different regions of the Mediterranean Sea characterized by different levels of primary productivity (Table 2.1.1).

Table 2.1.1 Overview of the projects and cruises that contributed to this study.

Project	Cruise	Date	Area	Depth
DESEAS (an exploratory survey to collect data of the exploited and virgin stocks of the deep-sea shrimp *Aristeus antennatus*	DESEAS	June 2009	South Balearic East Ionian Sea	600 1000 2000
	R/V Garcia del Cid			
BIOFUN (BIOdiversity and ecosystem FUNctioning in contrasting southern European deep-sea environments: from viruses to megafauna)	BF1	May-June 2009	South Balearic West Ionian Sea South of Crete	1200 2000 3000
	R/V Sarmiento de Gamboa			
RECS II (Integral Study of a Submarine Canyon in the western Mediterranean Sea, Blanes Canyon: Application to the exploitation of the deep-water rose shrimp)	RECS 1	Mar 2003	Catalan Sea: Blanes Canyon and West open slope; fishing ground	400 -1500
	RECS 3	Jul 2003		
	RECS 5	Nov 2003		
	RECS 7	May 2004		
	R/V Garcia del Cid			
PROMETEO (Integrated study of deep canyons and slopes of the western Mediterranean Sea: An essential habitat)	PR1	Oct 2008	Catalan Sea: Blanes Canyon and East adjacent slope	900-1500
	PR2	Feb 2009		
	PR3	May 2009		
	PR4	Sept 2009		
	PR5	Nov 2009		
	R/V Garcia del Cid			
DOS MARES (Deep-water submarine canyons and slopes in the Mediterranean and Cantabrian seas: from synchrony of external forcings to living resources)	DM1	Mar 2012	Catalan Sea: Blanes Canyon and East open slope	1500-2250
	DM3	Oct 2012		
	DM4	Apr 2013		
	R/V Garcia del Cid			

In the Catalan continental margin, incised by several submarine canyons, campaigns were conducted at the Blanes Canyon. This canyon is located in a region characterized by high seasonal and inter-annual variability in climate and oceanographic processes which affect the transport of sediment and organic matter towards the deep margin and basin. Moreover, the canyon upper course and the adjacent slope are targeted by crustacean trawlers exploiting the abundant populations of the shrimp *Aristeus antennatus* (Fig. 2.1.3). The campaigns performed in this area aimed to investigate the effects of organic matter and sediment transport through the Blanes Canyon on the benthic populations of meio-, macro- and megafauna, and in particular on the shrimp *Aristeus antennatus*.

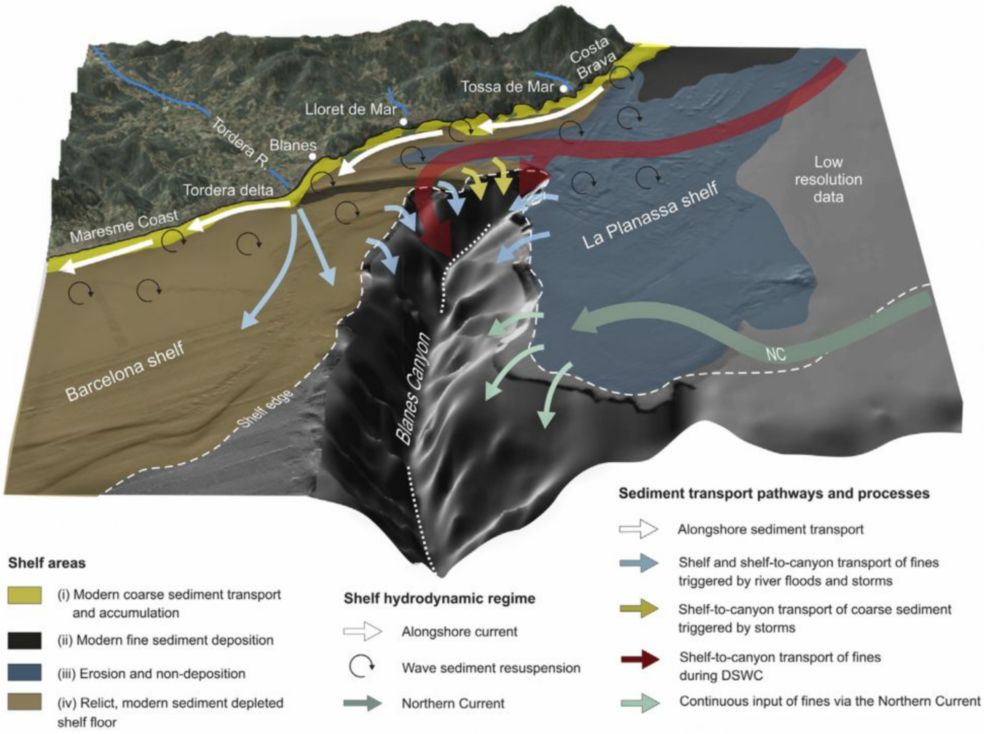

Figure 2.1.3 3D image of the Blanes Canyon illustrating the main domains in terms of sediment dynamics and sediment transport pathways across the shelf and into the canyon. From Canals et al., 2013.

Within the RECS II project four oceanographic cruises were conducted between 2003 and 2004. These aimed to sample the Blanes Canyon and the adjacent open slope fishing grounds. Additional sampling was obtained in the western and eastern side of the canyon. The depth ranged between 400 to 1500 m depth. Within the PROMETEO project five oceanographic cruises were conducted in the Blanes Canyon and the adjacent slope, from 2008 to 2009 covering the depth range 900-1500 m (plus one station at 1750 m). Three oceanographic cruises under the scope of DOS MARES project were conducted in the same area in 2012 and 2013 but covering the depth range from 1500 to 2250 m (Table 2.1.1).

The sorting and identification of the material from a sledge haul is usually very time consuming and in view of the large amount of material collected in the different cruises in the Catalan region, a selection of hauls was made based on the objectives and planned duration of the present PhD. The selection took into consideration the bathymetric range (the hauls included covered the maximum depth range available), location (both canyon and the adjacent open slope stations were included), and the temporal scale (intra and inter-annual). To minimize the seasonal effect on the suprabenthic fauna, the hauls performed in the autumn were selected to study the inter-annual variability of suprabenthic assemblages. Given this, only samples from RECS cruises, PROMETEO cruises 1, 4 and 5 and from DOS MARES cruise 3 were analysed in the present thesis. On total, data analysis of suprabenthos was assessed for the samples collected during the cruises DESEAS, BIOFUN, RECS 1, RECS 3, RECS 5 and RECS 7, PROMETEO 1, PROMETEO 4, PROMETEO 5 and DOSMARES 3 (Tables 2.1.1 and 2.1.2).

2.1.2.2 Sample collection

A total of 65 suprabenthic hauls (ca. 180 samples) were performed with a version of the Macer-GIROQ sledge (see Cartes et al., 1994 for a full description). Five hauls were excluded from the quantitative analyses due technical problems. Modified versions of this sledge (Brunel et al., 1978; Dauvin and Lorgere, 1989) have been employed in several suprabenthic studies in the Atlantic Ocean (e.g. Dauvin et al., 1995), Antarctic Ocean (e.g. San Vicente et al., 2009) and in the Mediterranean Sea (e.g. Cartes, 1998a). The version of the Macer-GIROQ sledge used consists of three rectangular nets (0.5 mm mesh size; opening of the net: 80 cm width and 40 cm height) arranged in three vertical layers which simultaneously sample at heights of 10-50, 55-95, and 100-140 cm above the seafloor (Fig. 2.1.4). A TSK flowmeter is attached to the middle mouth to measure the volume of water filtered. However due to inconsistencies in the values of flowmeters due to malfunction, these were not used to estimate the distance of each haul (see Chapters 2.2 to 2.5). The sledge was hauled over the ground around 30-60 min at a velocity approximately of 1.5-2 knots. Information on the position, depth, date and time of each haul is given in the Table 2.1.2. For each haul the distance trawled in meters is also indicated.

Table 2.1.2 Main characteristics of the hauls collected in the study areas of the Mediterranean Sea. OS: open slope; BC: Blanes Canyon.

	Sample code	**Site**	**Physiography**	**Date**	**Hour**[a]	**Depth**[a]	**Coordinates**[a]		**Dist.**[b]
				(d/m/y)	**(h:m)**	**(m)**	**Lat (N)**	**Lon (E)**	**(m)**
Chapter 2.2	DESEASP1	East Ionian	OS	28/06/2001	14:40	600	36° 50.95'	22°04.03'	926.0
	DESEASP2	East Ionian	OS	28/06/2001	17:34	1100	36° 45.77'	22°08.93'	1234.7
	DESEASP3	East Ionian	OS	28/06/2001	22.12	2150	36° 32.62'	22°07.63'	1852.0
	DESEASP4	South Balearic	OS	05/07/2001	12:47	2040	38° 05.50'	02°02.72'	1852.0
	DESEASP5	South Balearic	OS	05/07/2001	18:20	1000	38° 28.43'	01°53.25'	1234.7
	DESEASP6	South Balearic	OS	05/07/2001	21:17	600	38° 35.40'	01°52.30'	926.0
Chapter 2.3	BF1P2	South Balearic	OS	31/05/2009	14:20	1195	38°23.67'	1°49.39'	2039.9
	BF1P3	South Balearic	OS	31/05/2009	16:49	1130	38°26.12'	1°47.27'	1622.8
	BF1P4	South Balearic	OS	02/06/2009	01:29	2000	38°04.13'	1°59.50'	3632.0
	BF1P5	South Balearic	OS	04/06/2009	02:16	2850	38°41.47'	5°35.98'	3494.1
	BF1P6	West Ionian	OS	08/06/2009	05:20	1200	38°14.68'	16°35.89'	2817.7
	BF1P7	West Ionian	OS	08/06/2009	18:40	2000	37°39.41'	16°33.50'	3753.4
	BF1P8	West Ionian	OS	10/06/2009	03:54	3335	36°09.25'	16°27.93'	2946.5
	BF1P9	South Crete	OS	16/06/2009	02:50	1200	34°31.22'	25°46.97'	3646.3
	BF1P10	South Crete	OS	17/06/2009	03:24	2000	34°34.99'	25°51.81'	3704.0
	BF1P11	South Crete	OS	20/06/2009	02:50	2900	34°39.30'	26°06.14'	3735.8
Chapter 2.4	RECS1P4	Catalan Sea	BC	31/03/2003	03:37	466	41° 36.98'	02º 50.65'	2413.8
	RECS3P4	Catalan Sea	BC	09/07/2003	22:38	500	41º 36.77'	02º 50.67'	1389.0
	RECS5P2	Catalan Sea	BC	02/11/2003	00:23	487	41º 36.35'	02º 50.45'	972.3
	RECS7P5	Catalan Sea	BC	11/05/2004	06:45	510	41° 36.33'	02° 50.70'	1728.5
	RECS1P3	Catalan Sea	BC	31/03/2003	00:40	540	41° 29.30'	03° 01.48'	2592.8
	RECS3P3	Catalan Sea	BC	09/07/2003	19:24	557	41° 29.37'	03° 0.200'	2083.5
	RECS5P1	Catalan Sea	BC	01/11/2003	17:41	554	41° 29.28'	03° 0.500'	1404.4
	RECS7P4	Catalan Sea	BC	11/05/2004	04:23	560	41° 29.27'	03° 0.570'	1913.8
	RECS5P4	Catalan Sea	OS	06/11/2003	04:08	555	41° 24.05'	03° 17.28'	1674.6
	RECS1P1	Catalan Sea	OS	29/03/2003	21:23	711	41° 23.72'	03° 25.45'	1435.3
	RECS3P2	Catalan Sea	OS	09/07/2003	13:38	812	41° 22.67'	03° 23.47'	1666.8
	RECS5P3	Catalan Sea	OS	02/11/2003	12:48	781	41° 22.62'	03° 21.93'	2106.7
	RECS7P2	Catalan Sea	OS	10/05/2004	00:55	800	41° 22.60'	03° 22.95'	1890.6
	RECS5P6	Catalan Sea	OS	06/11/2003	11:50	910	41° 15.55'	02° 48.03'	1674.5
	RECS7P3	Catalan Sea	OS	11/05/2004	00:52	900	41° 15.43'	02° 46.42'	2052.6
	RECS3P6	Catalan Sea	OS	11/07/2003	06:15	1100	41° 06.18'	02° 25.55'	3704.0
	RECS3P5	Catalan Sea	OS	11/07/2003	01:05	1510	41° 19.65'	03° 11.37'	3241.0

Sample code	Site	Physiography	Date	Hour[a]	Depth[a]	Coordinates[a]		Dist.[b]
			(d/m/y)	(h:m)	(m)	Lat (N)	Lon (E)	(m)
RECS1P2	Catalan Sea	OS	30/03/2003	03:50	1500	41° 01.02'	02° 32.33'	3704.0
RECS5P5	Catalan Sea	OS	06/11/2003	06:45	1517	41° 19.32'	03° 11.78'	2916.9
RECS7P1	Catalan Sea	OS	10/05/2004	23:13	1510	41° 19.32'	03° 11.50'	2538.8
PR1P01	Catalan Sea	OS	27/10/2008	12:35	900	41°15.41'	2°48.25'	1234.7
PR1P05	Catalan Sea	OS	28/10/2008	02:09	1520	41°07.46'	2°52.39'	1566.5
PR4P01	Catalan Sea	OS	05/09/2009	11:30	1500	41°07.18'	2°51.89'	
PR4P02	Catalan Sea	OS	05/09/2009	14:24	1200	41°14.00'	2°49.99'	1055.6
PR4P03	Catalan Sea	OS	05/09/2009	16:12	900	41°15.77'	2°48.16'	2389.1
PR4P04	Catalan Sea	BC	11/09/2009	15:36	900	41°35.67'	2°51.06'	2284.1
PR4P10	Catalan Sea	OS	12/09/2009	07:57	900	41°15.71'	2°47.91'	2531.1
PR4P09	Catalan Sea	OS	12/09/2009	05:56	1050	41°15.41'	2°49.64'	2531.1
PR4P08	Catalan Sea	OS	12/09/2009	03:47	1200	41°13.92'	2°49.96'	2592.8
PR4P07	Catalan Sea	OS	12/09/2009	01:22	1350	41°09.99'	2°47.41'	2345.9
PR4P05	Catalan Sea	BC	11/09/2009	18:01	1500	41°28.30'	2°52.18'	3086.7
PR4P06	Catalan Sea	OS	11/09/2009	22:29	1500	41°07.47'	2°52.18'	1481.6
BF2P7	Catalan Sea	BC	03/11/2009	00:11	900	41°35.14'	2°50.92'	1852.0
BF2P9	Catalan Sea	OS	04/11/2009	11:31	1200	41°14.33'	2°50.10'	1852.0
BF2P8	Catalan Sea	OS	04/11/2009	-	1200	-	-	-
BF2P3	Catalan Sea	OS	01/11/2009	14:30	1500	41°07.58'	2°52.62'	1790.3
BF2P4	Catalan Sea	OS	01/11/2009	17:20	1350	41°10.28'	2°48.30'	-
BF2P4B	Catalan Sea	OS	01/11/2008	-	1350	-	-	-
BF2P5	Catalan Sea	BC	02/11/2009	20:20	1500	41°27.70'	2°52.38'	3086.7
BF2P2	Catalan Sea	OS	30/10/2009	18:55	1750	41°08.17'	2°58.72'	2469.3
BF2P1	Catalan Sea	OS	30/10/2009	15:26	2000	41°02.76'	3°03.27'	2037.2
DM2P11	Catalan Sea	BC	10/10/2012	22:44	1200	41º 30.60'	02º 51.1'	1731.6
DM2P3	Catalan Sea	OS	09/10/2012	15:06	1500	41º 07.40'	02º 50.4'	2024.9
DM2P10	Catalan Sea	BC	10/10/2012	19:37	1500	41º 26.20'	02º 53.20'	1521.7
DM2P5	Catalan Sea	OS	09/10/2012	21:37	2000	41º 04.0'	03º 06.60'	2963.2
DM2P8	Catalan Sea	BC	10/10/2012	11:47	2000	41º 13.9'	02º 54.60'	2864.4
DM2P6	Catalan Sea	OS	10/10/2012	02:00	2250	41º 56.8'	03º 16.90'	2963.2
DM2P7	Catalan Sea	BC	10/10/2012	06:48	2250	41º 03.4'	03º 15.3'	2963.2

a) beginning of the haul; b) bottom sampled by the sledge during the haul.

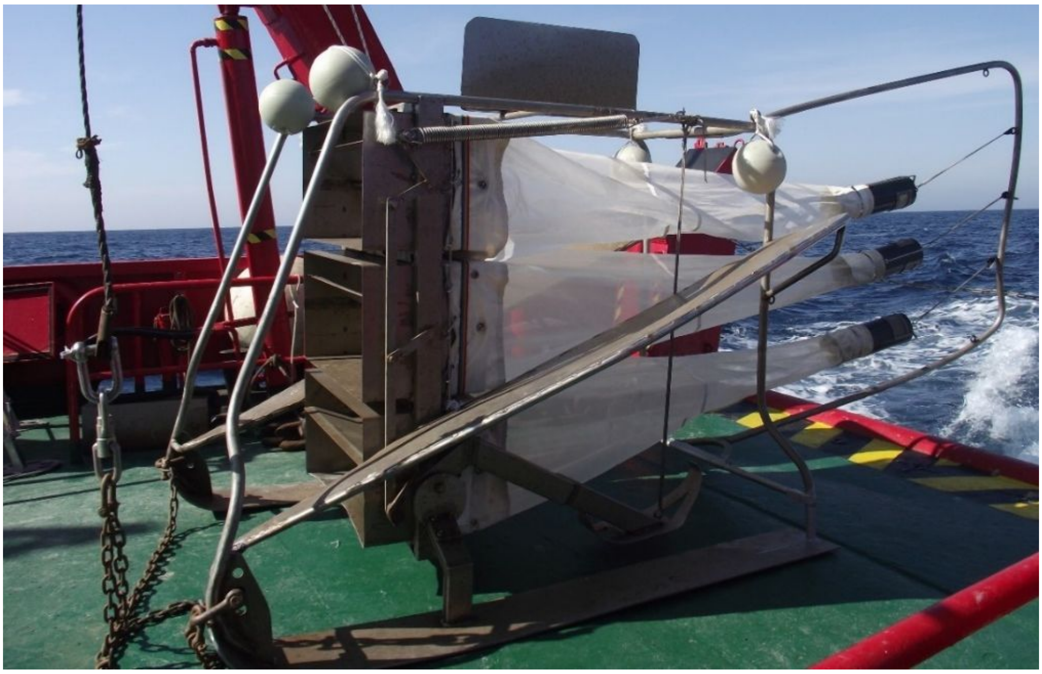

Figure 2.1.4 Modified version of the Macer-GIROQ sledge.

2.1.2.3 Sample processing

Sample processing was initiated on board by removing the fauna from the nets. The collected fauna from each net was sieved through a 500 µm mesh and fixed on board with 10% buffered formalin. In the lab the samples were sorted to various major taxa (e.g. Phylum, Class, Order) under a dissecting microscope and kept in 70% alcohol. For the purpose of this Thesis, only malacostracan crustaceans (larvae excluded) were considered. Given this, several groups that were also collected during the hauls were excluded from the analyses: 1) crustacean meiofaunal groups such as ostracods and copepods; 2) non-crustacean infaunal and epibenthic groups such as polychaetes, molluscs (aplacophorans, bivalves, gastropods), echinoderms (ophiuroids and crinoids) and sipunculans; 3) benthopelagic fishes; and 4) pelagic fauna such as tunicates, chaetognaths and gelatinous taxa (Fig. 2.1.5).

The crustaceans were counted and identified to the lowest taxonomic resolution, whenever possible to species level. The taxonomical work was carried out in CESAM at the University of Aveiro and in collaboration with specialists from other institutions. Specimens are held in the Biological Research Collection of the University of Aveiro (Department of Biology) and will be available for further ecologic, taxonomic and morphologic studies. Due to methodological constraints, the eucarids (euphausiids and decapods) from RECS campaigns were not available for counting and identification. For the isopods from two hauls of the DESEAS campaigns (haul 2 and 4) only the initial taxonomic assessment was considered because the samples were no longer available for further species identification.

Figure 2.1.5 Frequent crustacean meiofauna and larvae and non-crustacean groups collected with the Macer-Giroq sledge. A: Copepoda, B: Ostracoda, C: Chaetognatha, D, F: Tunicata, E: Pisces larvae, G: Pteropoda, H: Cephalopoda larvae, I, K: Decapoda larvae, J, M: Pisces, L: Gelatinous taxa.

2.1.2.4 Data analysis

The presence of each species is reported according to region (W: western, C: central and E: eastern), habitat (OS: open slope and BC: canyon) and depth. For each region and habitat characteristic species were highlighted following their constancy (Co, frequency of occurrence within a region or habitat expressed as percentage) and fidelity (Fi, partition of occurrences by different regions or habitats - the number of occurrences in a given region or habitat divided by the total number of occurrences, expressed as percentage). For constancy, species were classified as constant (C≥50.0%), accessory (50.0>C≥10.0%) and accidental (C≤10.0%). For fidelity, species were classified as exclusive (F>90.0%), elective (90≥F>67.0%), preferential (67.0≥F>50.0%), accompanying (50.0≥F>20.0%) and accidental or rare (F≤20.0%). The formulas, limits and terms considered in the scales of constancy and fidelity follow Retière (1979). Note that decapods and euphausiids were not accounted for in all samples.

A trophic guild was allocated to each taxon based on food source/foraging behavior, food type and size and feeding mode (adapted from MacDonald et al., 2010 with information compiled from Cartes, 1998b; Madurell et al., 2008; Fanelli et al., 2009). Food source (relative to foraging behaviour) of suprabenthic crustaceans was assigned to one of the following categories: water column/epibenthic (EP), seafloor surface (SR), and sediment subsurface (SS). Food type and size were described as sediment (sed), particulate organic matter (pom), microfauna (mic), meiofauna (mei), macrofauna (mac), phytodetritus (phy), zooplankton (zoo) and fish (fis). Feeding mode included detritus feeder (Dt), deposit feeder (De), suspension/filter feeder (Su), predator (Pr), scavenger (Sc), Suctorial parasite (Sp), grazer (Gr) and omnivore (Om) (for more details see MacDonald et al., 2010).

2.1.3 Results and Discussion

A total of 232 species of suprabenthic crustaceans was identified from the studied samples collected in the three Mediterranean basins (Table 2.1.3). The Amphipoda (99 species) and Cumacea (45 species) were the most speciose groups. Isopoda (26 species), Mysida (19 species) and Decapoda (26 species) showed intermediate values in number of species. The remaining taxa were represented by less than 10 species each (Lophogastrida: 2; Euphausiacea: 9; Leptostraca: 1; Tanaidacea: 5). Note that the orders

Decapoda, Euphausiacea and Leptostraca from RECS campaigns were not included in this analyses and the order Isopoda from two hauls of the DESEAS campaign were also not analysed to the highest taxonomic resolution, therefore the overall number of species of these groups may be underestimated. In general, the species found in the present study were also reported in previous studies from the Mediterranean continental slopes (see Table 3.1 for references in the General Discussion). The number of species found in the western, central and eastern basins (221, 110 and 67 species, respectively) fall within the range of the ones collected with a Macer-GIROQ sledge in the bathyal Catalan Sea (99 peracarid species, Cartes and Sorbe, 1993; 169 suprabenthic species (excluding isopods), Cartes et al., 1994; Cartes and Sorbe, 1995, 1997, 1999) and Balearic basin (104 peracarid species, Cartes et al., 2003; 187 suprabenthic species, Cartes et al., 2011). In the eastern Mediterranean basin, 66 species were collected with a plankton net (Madurell and Cartes, 2003).

In terms of abundances, more than 98 000 specimens were examined and ascribed to different taxonomic groups. Amphipoda (42 404 ind.) and Mysida (33 389 ind.) were the most abundant orders, followed by Isopoda (9595 ind.) and Cumacea (8240 ind.). Less abundant were Euphausiacea (3850 ind.), Decapoda (835 ind.) and finally Lophogastrida (230 ind.), Tanaidacea (34 ind.) and Leptostraca (25 ind.) (Fig. 2.1.6).

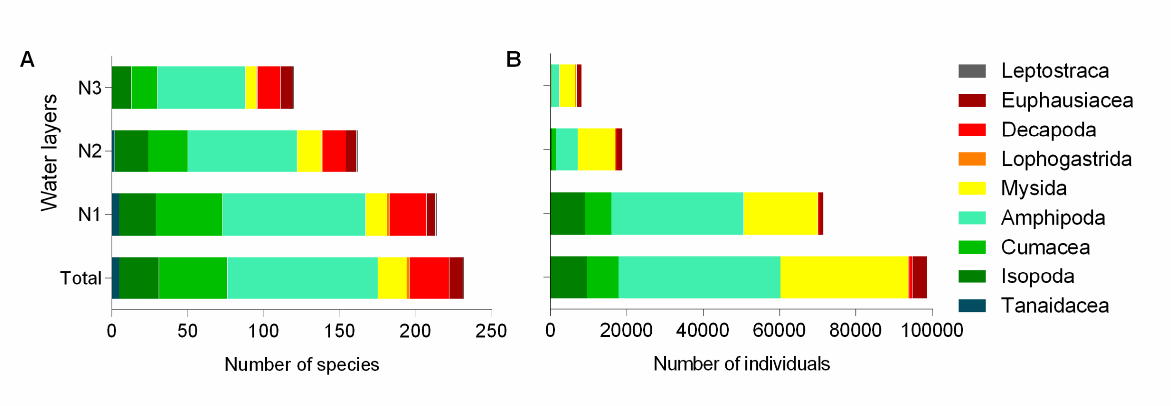

Figure 2.1.6 Number of species (A) and individuals (B) of the major taxonomic groups of suprabenthos from all samples taken in the Mediterranean Sea (N1: 10-50 cm, N2: 55-95 cm; N3: 100-140 cm; Total: 10-140 cm).

The broad assemblage of animals found in the suprabenthos is related to their distribution in space and not their phylogeny or exclusively functional attributes (Day et al., 1989); it is composed by species with a more limited relationship with the seafloor (e.g. downward extensions of mostly planktonic species), endo- and epibenthic species emerging from below the sediment surface and species living permanently in the water-sediment transition (Mees and Jones, 1997), resulting in a clear stratified distribution. Similarly to other studies using multinet sledges at bathyal depths (e.g. Cartes et al., 1994; Dauvin et al., 1995; Cunha et al., 1997; Sorbe, 1999), the suprabenthic organisms were concentrated in the close vicinity of the seafloor. Except for the order Tanaidacea, all faunal groups were found in the three water layers and only few species (18 species, mainly mysids, euphausiids and hyperid amphipods) occurred exclusively in the upper water layers. Approximately 45% of the species (105) were found throughouth the sampled water column (N1, N2 and N3) but the highest numbers of species and individuals occurred in the near-bottom water layer (N1: 214 species, 92.2%, 71 568 ind, 72.6%) (Fig. 2.1.6). Only the orders Lophogastrida and Euphausiacea showed relative high abundances in the 50-95 and 100–140 cm water layers. Globally, all faunal groups were found in all the sampling sites.

The species found were allocated to a total of 18 trophic guilds that occurred throughout the sampled water column, although with varying relative contributions. The orders Amphipoda and Decapoda were represented by the highest number of trophic guilds (10 and 9, respectively) followed by Isopoda (6), Cumacea (3), Mysida and Euphausiacea (2 each). Tanaidacea and Leptostraca were represented by one trophic guild (Fig. 2.1.7). The suprabenthic fauna was mostly represented by omnivores, predators and scavengers, relying on food sources both from the sediment and water column. To a less extent, grazers were well represented in the near-bottom water layer, whereas in the upper layers groups that rely on food sources from the sediment were less represented (Fig. 2.1.7). Overall, omnivores feeding on the water column food sources (particles and/or copepods) and predators feeding on copepods were the most abundant trophic groups.

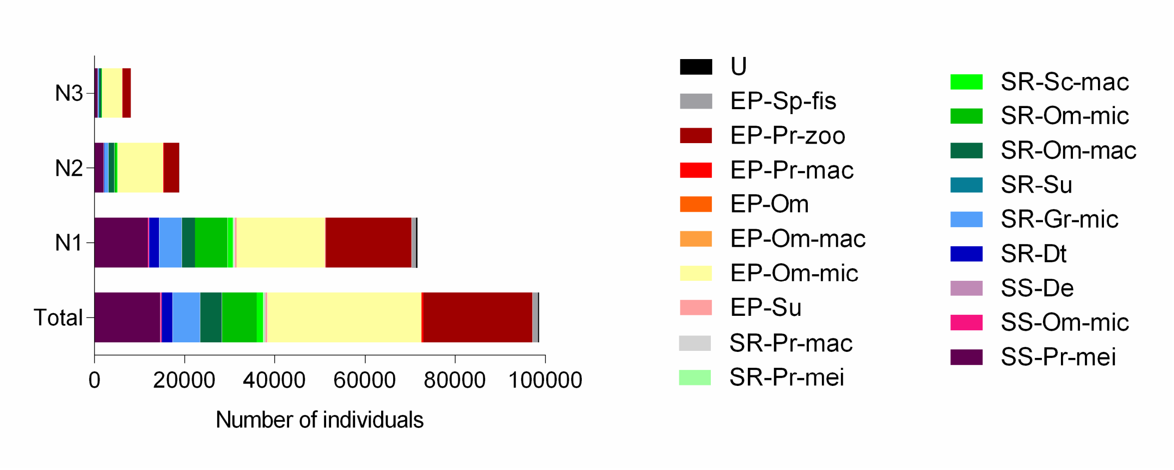

Figure 2.1.7 Number of trophic groups in the suprabenthos from all samples taken in the Mediterranean Sea (N1: 10-50 cm, N2: 55-95 cm; N3: 100-140 cm; Total: 10-140 cm). EP: water column/epibenthic; SR: seafloor surface; SS: sediment subsurface; mic: microfauna; mei: meiofauna; mac: macrofauna; zoo: zooplankton; fis: fish; Dt: detritus feeder; De: deposit feeder; Su: suspension/filter feeder; Pr: predator; Sc: scavenger; Sp: sectorial parasite; Gr: grazer; Om: omnivorous; U: unknown.

The complete species list is provided in Table 2.1.3. For consistency, the taxonomic classification is in accordance with the World Register of Marine Species (http://www.marinespecies.org). The bathymetric distributions and some remarks on the main crustacean taxa are included below.

Table 2.1.3 List of taxa found in the bathyal Mediterranean Sea. Taxonomic classification according to Worms – World of Marine Species (http://www.marinespecies.org accessed in November 2016). ind.: indetermined specimens at family or higher level. spp.: used when specimens of putative different species could not be separated within a given identified genus. AphiaID: taxon identifier in Worms.

Phyllum ARTHROPODA	**AphiaID**
Subphylum Crustacea	1066
Class Malacostraca Latreille, 1802	1071
Subclass Eumalacostraca	1086
Superorder Eucarida Calman, 1904	1089
Order Decapoda Latreille, 1803	1130
Decapoda ind.	1130
Decapoda sp A.	1130
Suborder Dendrobranchiata Spence Bate, 1888	106669
Superfamily Penaeoidea Rafinesque, 1815	106683
Family Aristeidae Wood-Mason in Wood-Mason & Alcock, 1891	106725
Genus *Aristeus* Duvernoy, 1840	106807
Aristeus antennatus (Risso, 1816)	107083
Family Benthesicymidae Wood-Mason in Wood-Mason & Alcock, 1891	106726
Genus *Gennadas* Spence Bate, 1881	106813
Gennadas elegans (Smith, 1882)	107095
Superfamily Sergestoidea Dana, 1852	106684
Family Sergestidae Dana, 1852	106731
Sergestidae ind.	106731
Genus *Allosergestes* Judkins & Kensley, 2008	513956
Allosergestes sargassi (Ortmann, 1893)	514114
Genus *Deosergestes* Judkins & Kensley, 2008	513957
Deosergestes corniculum (Krøyer, 1855)	514117
Genus *Eusergestes* Judkins & Kensley, 2008	513958
Eusergestes arcticus (Krøyer, 1855)	515738
Genus cf. *Sergia* Stimpson, 1860	106830
cf. ***Sergia robusta*** (Smith, 1882)	107136
Suborder Pleocyemata Burkenroad, 1963	106670
Infraorder Anomura MacLeay, 1838	106671
Superfamily Galatheoidea Samouelle, 1819	106685
Family Munididae Ahyong, Baba, Macpherson, Poore, 2010	562645
Genus *Munida* Leach, 1820	106835
Munida tenuimana Sars, 1872	107166

Superfamily Paguroidea Latreille, 1802	106687
Family Paguridae Latreille, 1802	106738
Genus *Pagurus* Fabricius, 1775	106854
Pagurus alatus Fabricius, 1775	107230
Infraorder Astacidea Latreille, 1802	106672
Superfamily Nephropoidea Dana, 1852	155750
Family Nephropidae Dana, 1852	106741
Genus *Nephropsis* Wood-Mason, 1872	106864
Nephropsis sp.	106864
Infraorder Axiidea de Saint Laurent, 1979	477324
Family Axiidae Huxley, 1879	106798
Genus *Calocaris* Bell, 1853	107071
Calocaris macandreae Bell, 1853	107726
Infraorder Brachyura Linnaeus, 1758	106673
Superfamily Portunoidea Rafinesque, 1815	106702
Family Geryonidae Colosi, 1923	106762
Genus *Geryon* Krøyer, 1837	106918
Geryon longipes A. Milne-Edwards, 1882	107373
Infraorder Caridea Dana, 1852	106674
Superfamily Crangonoidea Haworth, 1825	106712
Family Crangonidae Haworth, 1825	106782
Crangonidae ind.	**106782**
Genus *Aegaeon* Agassiz, 1846	107005
Aegaeon lacazei (Gourret, 1887)	107549
Genus *Philocheras* Stebbing, 1900	107010
Philocheras echinulatus (M. Sars, 1862)	107558
Genus *Pontophilus* Leach, 1817 [in Leach, 1815-1875]	107011
Pontophilus norvegicus (M. Sars, 1861)	107563
Pontophilus spinosus (Leach, 1816)	107564
Superfamily Oplophoroidea Dana, 1852	106714
Oplophoroidea ind.	106714
Family Acanthephyridae Spence Bate, 1888	585943
Genus *Acanthephyra* A. Milne-Edwards, 1881	107018
Acanthephyra eximia Smith, 1884	564909
Acanthephyra pelagica (Risso, 1816)	107581
Superfamily Nematocarcinoidea Smith, 1884	106713
Family Nematocarcinidae Smith, 1884	106784
Genus *Nematocarcinus* A. Milne-Edwards, 1881	107015
Nematocarcinus exilis (Spence Bate, 1888)	107574

Superfamily Pandaloidea Haworth, 1825	106716
Family Pandalidae Haworth, 1825	106789
Genus *Pandalina* Calman, 1899	107043
Pandalina profunda Holthuis, 1946	107648
Genus *Plesionika* Spence Bate, 1888	107046
Plesionika sp. A	107046
Superfamily Pasiphaeoidea Dana, 1852	106717
Family Pasiphaeidae Dana, 1852	106790
Genus *Pasiphaea* Savigny, 1816	107052
Pasiphaea multidentata Esmark, 1866	107676
Pasiphaea sivado (Risso, 1816)	107677
Superfamily Processoidea Ortmann, 1896	106718
Family Processidae Ortmann, 1896	106791
Genus *Processa* Leach, 1815	107054
Processa canaliculata Leach, 1815	107682
Infraorder Stenopodidea Spence Bate, 1888	106676
Family Stenopodidae Claus, 1872	106797
Genus *Richardina* A. Milne-Edwards, 1881	107065
Richardina sp. A	107065
Infraorder Polychelida Scholtz & Richter, 1995	383015
Family Polychelidae Wood-Mason, 1875	106793
Genus *Stereomastis* Spence Bate, 1888	107057
Stereomastis sculpta (Smith, 1880)	107700
Order Euphausiacea Dana, 1852	1128
Family Euphausiidae Dana, 1852	110671
Euphausiidae ind.	110671
Genus *Euphausia* Dana, 1850	110673
Euphausia sp. A	110671
Euphausia hemigibba Hansen, 1910	110686
Euphausia krohnii (Brandt, 1851)	110687
Genus *Meganyctiphanes* Holt & Tattersall, 1905	110674
Meganyctiphanes norvegica (M. Sars, 1857)	110690
Genus ***Nematoscelis*** G.O. Sars, 1883	110676
Nematoscelis cf. ***atlantica*** Hansen, 1916	110694
Nematoscelis megalops G.O. Sars, 1883	110695
Genus ***Stylocheiron*** G.O. Sars, 1883	110678
Stylocheiron spp.	110678
Stylocheiron cf. ***abbreviatum*** G.O. Sars, 1883	110699
Stylocheiron longicorne G.O. Sars, 1883	110703

Stylocheiron maximum Hansen, 1908	110704
Superorder Peracarida Calman, 1904	1090
Order Amphipoda Latreille, 1816	1135
Suborder Gammaridea Latreille, 1802	1207
Gammaridea ind.	1207
Family Ampeliscidae Krøyer, 1842	101364
Genus *Ampelisca* Krøyer, 1842	101445
Ampelisca cf. ***diadema*** (Costa, 1853)	101896
Genus cf. *Byblis* Boeck, 1871	101446
Byblis sp.	101446
Family Amphilochidae Boeck, 1871	101365
Genus *Amphilochoides* Sars, 1895	101448
Amphilochoides serratipes (Norman, 1869)	101963
Genus *Amphilochus* Bate, 1862	101450
Amphilochus planierensis Ledoyer, 1977	101970
Family Epimeriidae Boeck, 1871	101379
Genus *Epimeria* Costa, 1851	101506
Epimeria cornigera (Fabricius, 1779)	102145
Epimeria parasitica (M. Sars, 1858)	102147
Family Iphimediidae Boeck, 1871	101387
Genus *Iphimedia* Rathke, 1843	101554
Iphimedia sp. A	101544
Family Eusiridae Stebbing, 1888	101380
Eusiridae ind.	101380
Eusiridae sp. A	101380
Genus *Eusirus* Krøyer, 1845	101519
Eusirus leptocarpus Sars, 1895	102201
Eusirus longipes Boeck, 1861	102202
Genus ***Rhachotropis*** S.I. Smith, 1883	101528
Rhachotropis spp.	101528
Rhachotropis caeca Ledoyer, 1977	102226
Rhachotropis glabra Ledoyer, 1977	102230
Rhachotropis grimaldii (Chevreux, 1887)	102231
Rhachotropis integricauda Carausu, 1948	102235
Rhachotropis rostrata Bonnier, 1896	102242
Family Lepechinellidae Schellenberg, 1926	101392
Genus *Lepechinella* Stebbing, 1908	101578
Lepechinella manco Barnard, 1973	102454
Family Leucothoidae Dana, 1852	101393

Genus *Leucothoe* Leach, 1814	101580
Leucothoe incisa (Robertson, 1892)	102460
Leucothoe lilljeborgi Boeck, 1861	102462
Family Liljeborgiidae Stebbing, 1899	101394
Genus *Idunella* G.O. Sars, 1894	101581
Idunella pirata Krapp-Schickel, 1975	102478
Family Lysianassidae Dana, 1849	101395
Lysianassidae ind.	101395
Subfamily Lysianassinae Dana, 1849	177029
Genus *Lysianassa* Milne Edwards, 1830	101620
Lysianassa plumosa Boeck, 1871	102611
Genus *Socarnes* Boeck, 1871	101653
Socarnes sp.	101653
Subfamily Tryphosinae Lowry & Stoddart, 1997	176955
Genus *Hippomedon* Boeck, 1871	101610
Hippomedon bidentatus Chevreux, 1903	102569
Genus *Lepidepecreum* Bate & Westwood, 1868	101619
Lepidepecreum subclypeatum Ruffo & Schiecke, 1977	102601
Genus *Onesimoides* Stebbing, 1888	101630
Onesimoides mediterraneus Bellan-Santini, 1974	102634
Genus *Orchomene* Boeck, 1871	101633
Orchomene grimaldii Chevreux, 1890	102664
Orchomene cf. ***massiliensis*** Ledoyer, 1977	102670
Genus *Paracentromedon* Chevreux & Fage, 1925	101637
Paracentromedon crenulatus (Chevreux, 1900)	102701
Genus *Tryphosa* Boeck, 1871	101660
Tryphosa nana (Krøyer, 1846)	102748
Genus *Tryphosella* Bonnier, 1893	101661
Tryphosella spp.	101661
Tryphosella longidactyla Ruffo, 1985	102762
Tryphosella cf. ***nanoides*** (Lilljeborg, 1865)	102764
Tryphosella simillima Ruffo, 1985	102773
Genus *Tryphosites* G.O. Sars, 1895	101662
Tryphosites alleni Sexton, 1911	102778
Tryphosites longipes (Bate & Westwood, 1861)	102779
Family Melphidippidae Stebbing, 1899	101398
Genus *Melphidippella* Sars, 1894	101684
Melphidippella macra (Norman, 1869)	102860
Family Oedicerotidae Lilljeborg, 1865	101400

Oedicerotidae ind.	101400
Genus *Arrhis* Stebbing, 1906	101690
Arrhis mediterraneus Ledoyer, 1983	102869
Genus *Bathymedon* Sars, 1892	101691
Bathymedon spp.	101691
Bathymedon acutifrons Bonnier, 1896	102871
Bathymedon banyulsensis Ledoyer, 1983	102872
Bathymedon longirostris Jaume, Cartes & Sorbe, 1998	148544
Bathymedon monoculodiformis Ledoyer, 1983	102874
Genuns *Deflexilodes* Bousfield & Chevrier, 1996	236537
Deflexilodes acutipes (Ledoyer, 1983)	236538
Deflexilodes griseus (Della Valle, 1893)	236540
Genus *Monoculodes* Stimpson, 1853	101694
Monoculodes spp.	101694
Monoculodes sp. A	101694
Monoculodes cf. ***latissimanus*** Stephensen, 1931	102889
Monoculodes packardi Boeck, 1871	102892
Genus *Oediceroides* Stebbing, 1888	101697
Oediceroides pilosa Ledoyer, 1983	102903
Genus *Oediceropsis* Lilljeborg, 1865	101698
Oediceropsis brevicornis (Lilljeborg, 1865)	102904
Genus *Perioculodes* Sars, 1895	101701
Perioculodes longimanus (Bate & Westwood, 1868)	102915
Genus *Synchelidium* Sars, 1895	101704
Synchelidium haplocheles (Grube, 1864)	102924
Genus *Westwoodilla* Bate, 1862	101705
Westwoodilla caecula (Bate, 1857)	102932
Westwoodilla rectirostris (Della Valle, 1893)	102937
Family Opisidae Lowry & Stoddart, 1995	176953
Genus *Normanion* Bonnier, 1893	101629
Normanion ruffoi Diviacco & Vader, 1988	102632
Family Pardaliscidae Boeck, 1871	101401
Parladascidae ind.	101401
Genus *Arculfia* Barnard, 1961	101706
Arculfia trago Karaman, 1986	102938
Genus *Halice* Boeck, 1871	101707
Halice abyssi Boeck, 1871	102939
Halice walkeri (Ledoyer, 1973)	102941
Genus *Nicippe* Bruzelius, 1859	101709

Nicippe tumida Bruzelius, 1859	102944
Genus *Pardalisca* Krøyer, 1842	101710
Pardalisca brachydactyla Bellan-Santini, 1985	102946
Pardalisca mediterranea Bellan-Santini, 1984	102948
Family Phoxocephalidae Sars, 1891	101403
Subfamily Harpiniinae Barnard & Drummond, 1978	176844
Genus *Harpinia* Boeck, 1876	101716
Harpinia spp.	101716
Harpinia dellavallei Chevreux, 1910	102966
Harpinia truncata Sars, 1891	102976
Subfamily Phoxocephalinae G.O. Sars, 1891	549026
Genus *Metaphoxus* Bonnier, 1896	101720
Metaphoxus simplex (Bate, 1857)	102984
Family Podoprionidae Lowry & Stoddart, 1996	550205
Genus cf. *Podoprion* Chevreux, 1891	101646
cf. ***Podoprion*** sp. A	101646
Podoprion bolivari Chevreux, 1891	102711
Family Scopelocheiridae Lowry & Stoddart, 1997	176791
Subfamily Scopelocheirinae Kilgallen & Lowry, 2015	852214
Genus *Scopelocheirus* Bate, 1856	101652
Scopelocheirus hopei (Costa, 1851)	102720
Family Sebidae Walker, 1908	101407
Genus *Seba* Bonnier, 1896	101746
Seba aloe Karaman, 1971	103081
Family Sophrosynidae Lowry & Stoddart, 2010	463589
Genus *Sophrosyne* Stebbing, 1888	101655
Sophrosyne sp. A	101655
Sophrosyne hispana (Chevreux, 1888)	102728
Family Stegocephalidae Dana, 1855	101408
Subfamily Andaniexinae Berge & Vader, 2001	176891
Genus *Mediterexis* Berge & Vader, 2001	236544
Mediterexis mimonectes (Ruffo, 1975)	236545
Subfamily Stegocephalinae Dana, 1855	176905
Genus *Stegocephaloides* Sars, 1895	101757
Stegocephaloides christianiensis Boeck, 1871	103102
Family Synopiidae Dana, 1853	101410
Synopiidae ind.	101410
Genus *Bruzelia* Boeck, 1871	101774
Bruzelia typica Boeck, 1871	103182

Genus *Ileraustroe* J.L. Barnard, 1972	101775
Ileraustroe ilergetes (Barnard, 1964)	103183
Genus P*seudotiron* Chevreux, 1895	101776
Pseudotiron bouvieri Chevreux, 1895	103184
Genus *Syrrhoe* Goës, 1866	101778
Syrrhoe spp.	101778
Syrrhoe cf. ***affinis*** Chevreux, 1908	103186
Syrrhoe angulipes Ledoyer, 1977	103187
Genus *Syrrhoites* Sars, 1895	101779
Syrrhoites cf. ***cornuta*** Bellan-Santini, 1984	103191
Syrrhoites cf. ***pusilla*** Enequist, 1949	103192
Family Uristidae Hurley, 1963	176808
Genus *Caeconyx* Barnard & Karaman, 1991	101597
Caeconyx caeculus (G.O. Sars, 1891)	102543
Genus *Tmetonyx* Stebbing, 1906	101658
Tmetonyx cf**. *dilatata*** (Chevreux, 1903)	530717
Tmetonyx similis (Sars, 1891)	102742
Suborder Hyperiidea Milne Edwards, 1830	1205
Hyperiidea ind.	1205
Infraorder Physocephalata Bowman & Gruner, 1973	155692
Superfamily Phronimoidea Bowman & Gruner, 1975	155696
Family Hyperiidae Dana, 1852	101417
Genus *Hyperia* Latreille, 1823	101796
Hyperia sp.A	101796
Genus *Themisto* Guérin, 1825	101800
Themisto sp.A	101800
Family Lestrigonidae Zeidler, 2004	414835
Genus *Hyperioides* Chevreux, 1900	101797
Hyperioides sp. A	101797
Hyperioides longipes Chevreux, 1900	103255
Family Phronimidae Dana, 1852	101420
Genus *Phronima* Latreille, 1802	101804
Phronima atlantica Guérin-Méneville, 1836	103271
Phronima sedentaria (Forskål, 1775)	103272
Genus *Phronimella* Claus, 1871	236610
Phronimella sp. A	236610
Family Phrosinidae Dana, 1852	101421
Genus *Anchylomera* Milne Edwards, 1830	236612
Anchylomera blossevillei Milne Edwards, 1830	236613

Genus *Phrosina* Risso, 1822	101805
Phrosina semilunata Risso, 1882	103273
Genus *Primno* Guérin-Méneville, 1836	101806
Primno macropa Guérin-Méneville, 1836	180759
Superfamily Platysceloidea Bate, 1862	155698
Family Lycaeidae Claus, 1879	158321
Lycaeidae sp. A	158321
Family Oxycephalidae Bate, 1861	196118
Ocycephalidae sp. A	196118
Genus *Rhabdosoma* White, 1847	205957
Rhabdosoma brevicaudatum Stebbing, 1888	236590
Family Platyscelidae Bate, 1862	101422
Genus *Platyscelus* Bate, 1861	101807
Platyscelus serratulus Stebbing, 1888	236623
Superfamily Vibilioidea Bowman & Gruner, 1973	155694
Family Vibiliidae Dana, 1852	101426
Genus *Vibilia* Milne Edwards, 1830	101812
Vibilia armata Bovallius, 1887	236632
Infraorder Physosomata	155686
Superfamily Scinoidea Bowman & Gruner, 1973	155687
Family Scinidae Stebbing, 1888	101424
Genus *Scina* Prestandrea, 1833	101810
Scina sp. A	101810
Suborder Senticaudata Lowry & Myers, 2013	719424
Infraorder Carangoliopsida Bousfield, 1977	719425
Superfamily Carangoliopsoidea Bousfield, 1977	744657
Family Carangoliopsidae Bousfield, 1977	101373
Genus *Carangoliopsis* Ledoyer, 1970	101482
Carangoliopsis spinulosa Ledoyer, 1970	102074
Infraorder Corophiida Leach, 1814 (sensu Lowry & Myers, 2013)	719474
Superfamily Aoroidea Stebbing, 1899	716532
Family Aoridae Stebbing, 1899	101368
Aoridae sp. A	101368
Genus *Lembos* Bate, 1857	101469
Lembos sp. A	101469
Superfamily Caprelloidea Leach, 1814	196121
Family Caprellidae Leach, 1814	101361
Genus *Parvipalpus* Mayer, 1890	101434
Parvipalpus major Carausu, 1941	101860

Superfamily Hadzioidea S. Karaman, 1943 (Bousfield, 1983)	719496
Family Eriopisidae Lowry & Myers, 2013	719498
Genus *Psammogammarus* Karaman, 1955	101681
Psammogammarus caecus Karaman, 1955	102852
Order Cumacea Krøyer, 1846	1137
Cumacea ind.	1137
Family Bodotriidae T. Scott, 1901	110378
Bodotriidae ind.	110378
Genus *Cyclaspis* Sars, 1865	110388
Cyclaspis longicaudata Sars, 1865	110446
Genus *Iphinoe* Bate, 1856	110391
Iphinoe cf. ***serrata*** Norman, 1867	110460
Genus *Vaunthompsonia* Bate, 1858	110394
Vaunthompsonia sp. A	110394
Vaunthompsonia caeca Bonnier, 1895	181887
Family Diastylidae Bate, 1856	110380
Genus *Diastylis* Say, 1818	110398
***Diastylis* spp.**	110398
Diastylis cf. ***cornuta*** (Boeck, 1864)	110474
Diastylis doryphora Fage, 1940	181941
Diastylis cf. ***jonesi*** Reyss, 1972	110480
Diastylis richardi Fage, 1929	181979
Genus *Diastyloides* G.O. Sars, 1900	110399
Diastyloides serratus (Sars G.O., 1865)	110497
Genus *Leptostylis* G.O. Sars, 1869	110403
Leptostylis spp. (several species)	110403
Leptostylis sp. A	110403
Leptostylis cf. ***macrura*** Sars, 1870	110504
Leptostylis cf. ***gamoi*** Reyss, 1972	182050
Genus *Makrokylindrus* Stebbing, 1912	110404
Makrokylindrus spp.	110404
Makrokylindrus (Makrokylindrus) aegaeus Reyss, 1974	110606
Makrokylindrus (Adiastylis) josephinae (Sars, 1871)	110601
Makrokylindrus (Adiastylis) insignis (Sars, 1871)	110600
Makrokylindrus (Adiastylis) longipes (Sars, 1871)	110603
Genus *Vemakylindrus* Bacescu, 1961	110405
Vemakylindrus charcoti (Reyss, 1974)	110507
Family Lampropidae Sars, 1878	110381
Genus *Hemilamprops* G.O. Sars, 1883	110407

Hemilamprops cristatus (Sars G.O., 1870)	110511
Genus *Platysympus* Stebbing, 1912	110411
Platysympus typicus (Sars, 1870)	110522
Family Leuconidae Sars, 1878	110382
Leuconidae ind.	110382
Genus *Eudorella* Norman, 1867	110412
Eudorella spp.	110412
Eudorella sp. A	110412
Eudorella cf. ***nana*** Sars, 1879	110531
Genus *Leucon* Krøyer, 1846	110414
Leucon spp.	110414
Leucon sp. A	110414
Leucon (Leucon) cf. ***affinis*** Fage, 1951	160615
Leucon (Epileucon) longirostris Sars, 1871	110613
Leucon (Crymoleucon) macrorhinus Fage, 1951	110610
Leucon (Leucon) mediterraneus Sars, 1878	110617
Family Nannastacidae Bate, 1866	110383
Nannastacidae ind.	110383
Genus *Campylaspis* G.O. Sars, 1865	110415
Campylaspis spp.	110415
Campylaspis sp. A	110415
Campylaspis sp. B	
Campylaspis glabra Sars, 1878	110543
Campylaspis horridoides Stephensen, 1915	110546
Campylaspis nitens Bonnier, 1896	110553
Campylaspis cf. ***rostrata*** Calman, 1905	110554
Campylaspis cf. ***squamifera*** Fage, 1929	110557
Campylaspis sulcata Sars, 1870	110558
Campylaspis verrucosa Sars, 1866	110560
Campylaspis vitrea Calman, 1906	110561
Genus *Cumella* G.O. Sars, 1865	110416
Cumella sp. A	110416
Cumella sp. B	110416
Cumella gracilima Calman, 1905	489232
Genus *Cumellopsis* Calman, 1905	110417
Cumellopsis puritani Calman, 1906	110570
Genus *Nannastacus* Bate, 1865	110418
Nannastacus sp. A	110418
Genus *Styloptocuma* Bacescu & Muradian, 1974	110424

aff. ***Styloptocuma dayae*** (Jones, 1984)	182543
Genus *Procampylaspis* Bonnier, 1896	110421
Procampylaspis sp. A	110421
Procampylaspis armata Bonnier, 1896	110581
Procampylaspis bonnieri Calman, 1906	110584
Order Isopoda Latreille, 1817	1131
Isopoda ind.	1131
Suborder Asellota Latreille, 1802	13794
Superfamily Janiroidea Sars, 1897	155716
Family Desmosomatidae G.O. Sars, 1897	118250
Desmosomatidae ind.	118250
Genus *Chelator* Hessler, 1970	118317
Chelator sp. A	118317
Genus *Eugerda* Meinert, 1890	118323
Eugerda spp.	118323
Eugerda sp. A	118323
Eugerda cf. ***tenuimana*** (Sars G.O., 1866)	118559
Genus *Eugerdella* Kussakin, 1965	118324
Eugerdella pugilator Hessler, 1970	118569
Genus *Mirabilicoxa* Hessler, 1970	118325
Mirabilicoxa sp. A	118325
Family Ischnomesidae Hansen, 1916	118256
Genus Ischnomesus Richardson, 1908	118358
Ischnomesus bispinosus (Sars, 1866)	118694
Family Janirellidae Menzies, 1956	118257
Genus *Janirella* Bonnier, 1896	118360
Janirella nanseni Bonnier, 1896	118707
Family Munnopsidae Lilljeborg, 1864	118264
Munnopsidae ind.	118264
Subfamily Eurycopinae Hansen, 1916	325351
Genus *Belonectes* Wilson & Hessler, 1981	118338
Belonectes parvus (Bonnier, 1896)	118606
Genus Disconectes Wilson & Hessler, 1981	118339
Disconectes spp.	118339
Disconectes sp. A	118339
Disconectes furcatus (Sars G.O., 1870)	118608
Disconectes cf. ***furcatus*** (Sars G.O., 1870)	118608
Disconectes cf. ***latirostris*** (G. O. Sars, 1883)	118609
Disconectes phalangium (Sars, 1864)	118610

Subfamily Iyarachninae Hansen, 1916	325353
Genus *Aspidarachna* G.O. Sars, 1897	148670
Aspidarachna cf. ***sekhari*** (George & Menzies, 1968)	257621
Genus *Ilyarachna* G.O. Sars, 1870	118354
Ilyarachna spp.	118354
Ilyarachna sp. A	118354
Ilyarachna calidus George & Menzies 1968	a)
Ilyarachna cf. ***calidus*** George & Menzies 1968	a)
Ilyarachna cf. ***longicornis*** (G.O. Sars, 1864)	118677
Genus *Munnopsurus* Richardson, 1912	118343
Munnopsurus atlanticus (Bonnier, 1896)	118635
Suborder Cymothoida Wägele, 1989	292941
Superfamily Anthuroidea Leach, 1914	292944
Family Anthuridae Leach, 1814	118244
Anthuridae sp. A	118244
Superfamily Cymothooidea Leach, 1814	292946
Cymothooidea sp. A	292946
Family Aegidae White, 1850	118272
Genus ***Aegiochus*** Bovallius, 1885	293761
Aegiochus incisa (Schiödte & Meinert, 1879)	118821
Family Cirolanidae Dana, 1852	118273
Genus *Eurydice* Leach, 1815	118401
Eurydice grimaldii Dollfus, 1888	118848
Genus *Natatolana* Bruce, 1981	118404
Natatolana borealis (Lilljeborg, 1851)	118859
Natatolana caeca (Dollfus, 1903)	118860
Family Gnathiidae Leach, 1814	118278
Gnathiidae sp.A	118278
Order Lophogastrida Boas, 1883	149669
Family Eucopiidae G.O. Sars, 1885	119819
Genus *Eucopia* Dana, 1852	119825
Eucopia unguiculata (Willemoes-Suhm, 1875)	119921
Family Lophogastridae G.O. Sars, 1870	119821
Genus Lophogaster M. Sars, 1857	119828
Lophogaster sp. A	119828
Order Mysida Boas, 1883	149668
Mysida ind.	149668
Family Mysidae Haworth, 1825	119822
Mysidae sp. A	

Subfamily Boreomysinae Holt & Tattersall, 1905	154152
Genus *Boreomysis* G.O. Sars, 1869	119842
Boreomysis arctica (Krøyer, 1861)	119962
Boreomysis megalops G.O. Sars, 1872	119967
Subfamily Erythropinae Hansen, 1910	596590
Erythropinae ind.	596590
Genus *Amblyops* G.O. Sars, 1872	119832
Amblyops trisetosus Nouvel & Lagardère, 1976	119948
Genus *Calyptomma* W. Tattersall, 1909	119846
Calyptomma puritani W. Tattersall, 1909	119979
Genus *Dactylamblyops* Holt & Tattersall, 1906	19851
Dactylamblyops sp. A	19851
Dactylamblyops corberai San Vicente & Cartes, 2011	571543
Genus *Erythrops* G.O. Sars, 1869	119856
Erythrops spp.	119856
Erythrops neapolitanus Colosi, 1929	446451
Genus *Euchaetomera* G.O. Sars, 1883	119857
Euchaetomera intermedia Nouvel, 1942	120008
Genus *Paramblyops* Holt & Tattersall, 1905	119891
Paramblyops rostratus Holt & Tattersall, 1905	446463
Genus ***Parerythrops*** G.O. Sars, 1869	119894
Parerythrops lobiancoi W. Tattersall, 1909	120168
Genus *Parapseudomma* Nouvel & Lagardère, 1976	119893
Parapseudomma calloplura (Holt & Tattersall, 1905)	120165
Genus *Pseudomma* G.O. Sars, 1870	119900
***Pseudomma* spp.**	119900
Pseudomma affine G.O. Sars, 1870	120182
Pseudomma cf. ***kruppi*** W. Tattersall, 1909	120188
Pseudomma cf. ***nanum*** Holt & Tattersall, 1906	120189
Subfamily Gastrosaccinae Norman, 1892	148702
Genus *Haplostylus* Kossmann, 1880	119860
Haplostylus lobatus (Nouvel, 1951)	148703
Subfamily Leptomysinae Czerniavsky, 1882	596591
Genus *Mysideis* G.O. Sars, 1869	119882
Mysideis parva Zimmer, 1915	120081
Subfamily Mysidellinae Czerniavsky, 1882	148707
Genus *Mysidella* G.O. Sars, 1872	119883
Mysidella spp.	119883
Mysidella biscayensis Lagardère & Nouvel, 1980	120082

Subfamily Mysinae Haworth, 1825 (Subfamily)	148706
Genus *Hemimysis* G.O. Sars, 1869	119861
Hemimysis abyssicola G.O. Sars, 1869	120024
Order Tanaidacea Dana, 1849	1133
Suborder Apseudomorpha Sieg, 1980	136150
Superfamily Apseudoidea Leach, 1814	148688
Apseudoidae ind.	148688
Family Apseudidae Leach, 1814	136153
Subfamily Apseudinae Leach, 1814	136166
Genus *Apseudes* Leach, 1814	136185
Apseudes spinosus (M. Sars, 1858)	136284
Subfamily Leviapseudinae Sieg, 1983	136167
Genus *Leviapseudes* Sieg, 1983	136192
Leviapseudes spp.	136192
Leviapseudes cf. ***segonzaci*** Bacescu, 1981	136308
Suborder Tanaidomorpha Sieg, 1980	136152
Superfamily Paratanaoidea Lang, 1949	148687
Paratanaoidea sp. A	148687
Family Agathotanaidae Lang, 1971	237594
Genus *Paranarthrura* Hansen, 1913	136225
Paranarthrura lusitanus Bird & Holdich, 1989	136383
Family Colletteidae Larsen & Wilson, 2002	237595
Genus *Collettea* Lang, 1973	136208
Collettea sp. A	
Subclass Phyllocarida Packard, 1879	146995
Order Leptostraca	146996
Leptostraca sp. A	146996

a) Species not reported in WORMS

Amphipoda

Amphipoda was the most species rich and abundant order representing nearly half of the total number of species. Most of the specimens were ascribed to the Sub-order Gammaridea (>98%) whilst few individuals were ascribed to the Sub-orders Senticaudata and Hyperiidea. Noteworthy is that despite the low number of individuals of the sub-order Hyperiidea, they were well represented in terms of number of species (16 species) (Fig. 2.1.8). The most abundant and species rich Gammaridea families were Eusiridae (36.7% of Amphipoda sampled; 8 species), Oedicerotidae (30.2%; 16), Lysianassidae (14.2%; 23) and Synopiidae (7.8%; 7). The most abundant species (by decreasing abundance) were *Rhachotropis caeca*, *Synchelidium haplocheles*, *Scopelocheirus hopei*, *Rhachotropis glabra*, *Bathymedon longirostris*, *Bathymedon acutifrons*, *Mediterexis mimonectes*, *Ileraustroe ilergetes*, *Bathymedon banyulsensis*, *Bruzelia typica* and *Rhachotropis rostrata* (Fig. 2.1.9).

Regarding the bathymetric distribution of the sub-order Hyperiidea, nine species (e.g. *Anchylomera blossevillei, Hyperioides longipes*) were found exclusively deeper than 1000 m while 5 species (e.g. *Vibilia armata*, *Primno macropa*) were found in a wide bathymetric range (ca. 500-3000 m) and only one species was found in the entire bathymetric range (*Primno macropa*) (Fig. 2.1.10). For the sub-order Senticaudata only one species was found in a wide bathymetric range (from 487 to 2250 m; *Carangoliopsis spinulosa*) and three species (e.g. *Parvipalpus major*) were found shallower than 1000 m depth (Fig. 2.1.11). For the sub-order Gammaridea, eight species (e.g. *Epimeria cornigera*, *Rhachotropis caeca*, *Tryphosa nana*, *Scopelocheirus hopei*) were collected in the entire bathymetric range and eight species (e.g. *Orchomene grimaldi, Vibilia armata*) occurred throughout a wide bathymetric range (from ca. 500-3000 m). A high number (23 species, e.g. *Rhachotropis glabra*, *Leucothoe lilljeborgi*, *Bathymedon longirostris*) occurred from 466 to 2250 m depth. Only four species (e.g. *Lysianassa plumosa*, *Onesimoides mediterraneus*) were found exclusively deeper than 1000 m and only ten (e.g. *Nicippe tumida*, *Podoprion bolivari*, *Pardalisca brachydactyla*, *Rhachotropis integricauda*, *Westwoodilla rectirostris*) were found exclusively shallower than 600 m (Fig. 2.1.12).

Amphipods were composed by diversified trophic guilds with different swimming capacities, that ranged from species more closely related to the sediment (e.g. oedicerotids) and others with relatively high swimming capacities (e.g. eusirids, lysianassids) (Cartes and Sorbe, 1999).

Comparing the assemblage composition of this study with the one found in a close location, in the Merenguera Canyon (Cartes and Sorbe, 1999), differences were found: endobenthic amphipods characterized by very low swimming capabilities, such as the Carangoliopsidae *Carangoliopsis spinulosa*, the Oedicerotidae *Synchelidium maculatum*, the Haustoriidae *Urothoe corsica* and several Phoxocephalidae species were abundant at this location (Cartes and Sorbe, 1999) while at the studied assemblage these species were absent or few individuals were found. Moreover, only 12 lysianassids were found in the Merenguera Canyon in contrast to the present work that reported 19 lysianassids in the Catalan slopes. The potential reason for such differences are explained in Chapter 2.4.

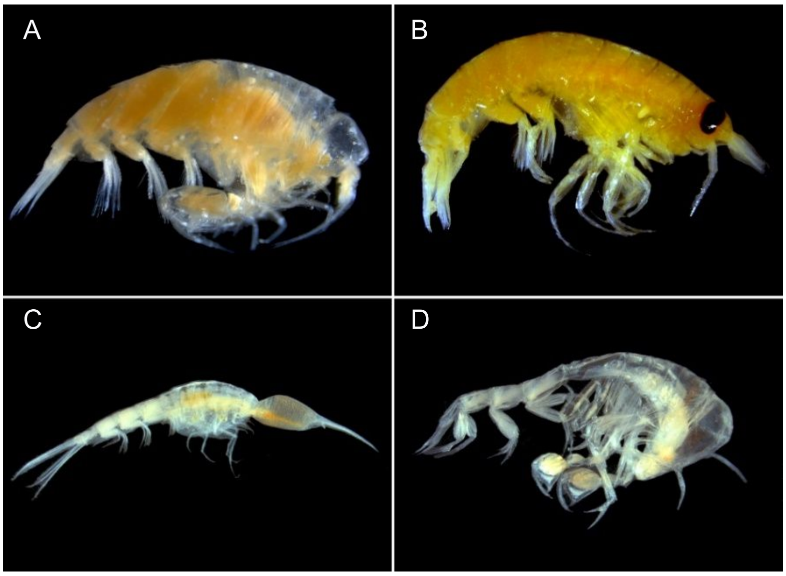

Figure 2.1.8 Specimens of hyperiids collected in the bathyal Mediterranean Sea. A: *Primno macropa* B: *Vibilia armata*; C: Oxycephalidae, D: Phronimidae.

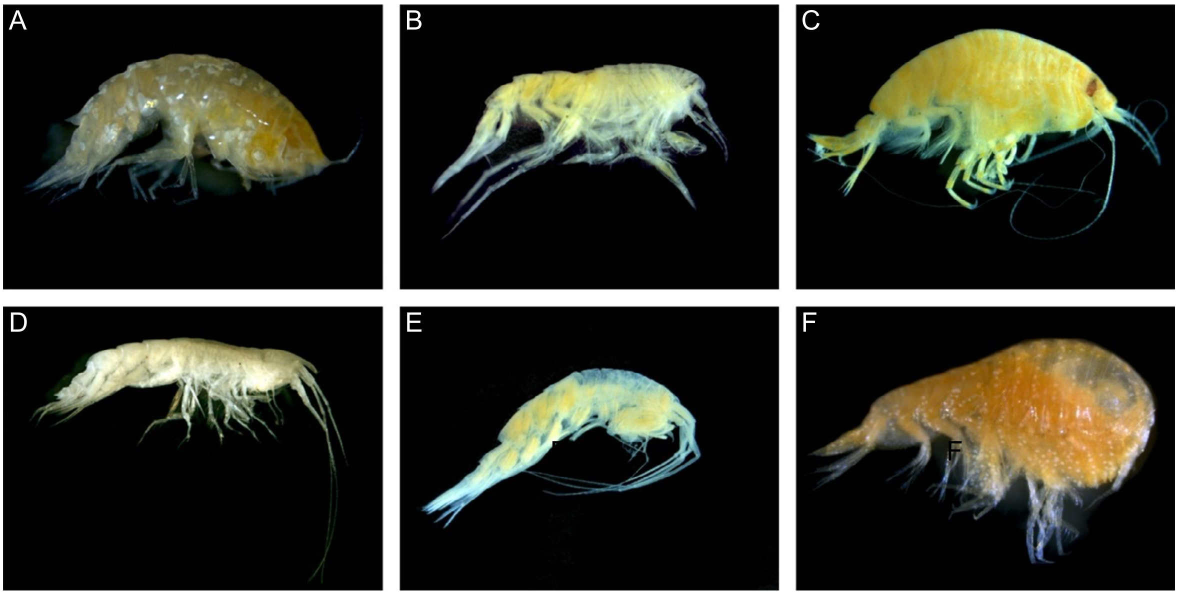

Figure 2.1.9 Specimens of gammarids collected in the bathyal Mediterranean Sea. A: *Bruzelia typical*, B: *Synchelidium haplocheles*, C: *Scopelocheirus hopei* D: *Bathymedon longirostris* E: *Rhachotropis* sp. F: *Mediterexis mimonectes.*

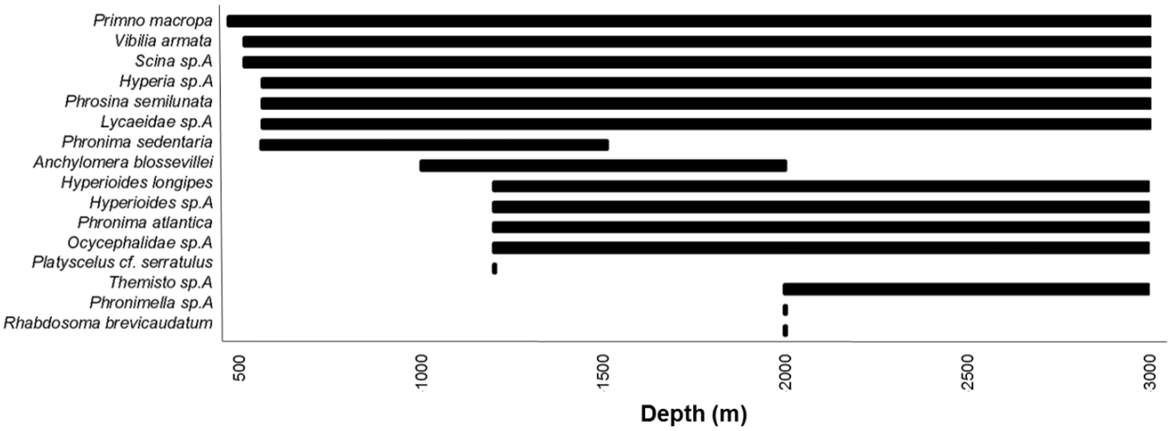

Figure 2.1.10 Bathymetric ranges of the species of the sub-order Hyperiidea collected in the bathyal Mediterranean Sea. Undetermined specimens are not included.

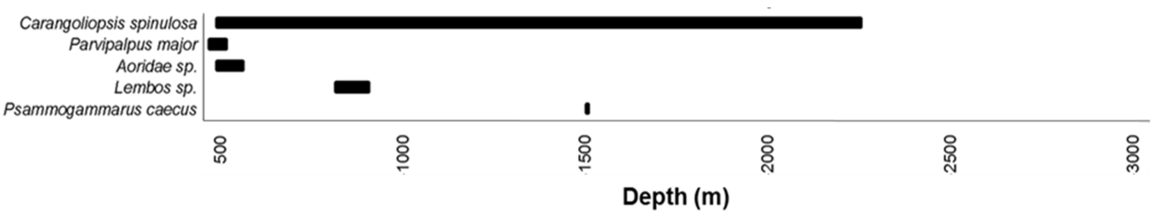

Figure 2.1.11 Bathymetric ranges of the species of the sub-order Senticaudauta collected in the bathyal Mediterranean Sea.

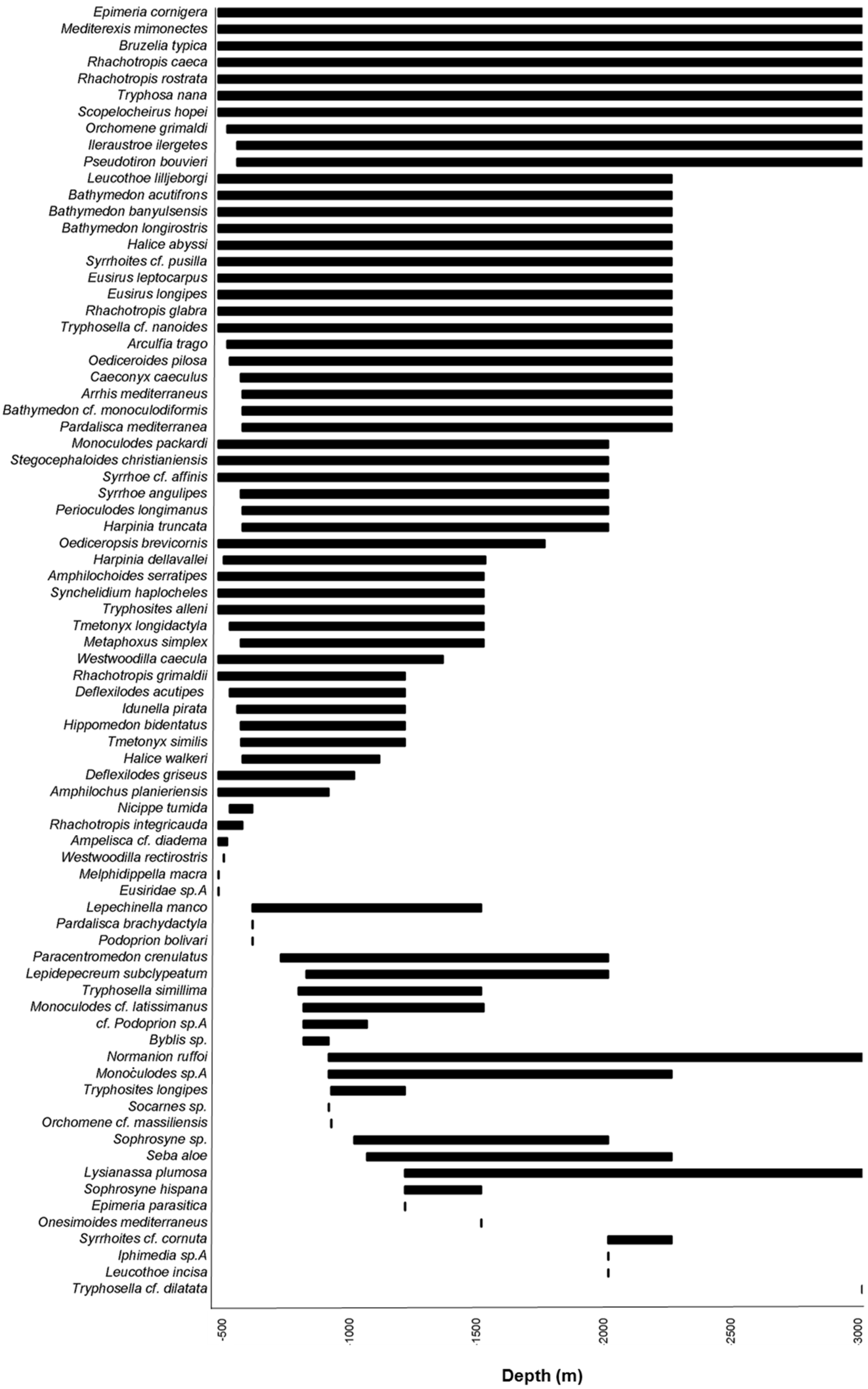

Figure 2.1.12 Bathymetric ranges of the species of the sub-order Gammaridea collected in the bathyal Mediterranean Sea. Undetermined specimens are not included.

Cumacea

Cumacea, the second most speciose group, is an important component of suprabenthic communities in this region (Cartes and Sorbe, 1997). Among this Order, six families were represented in the samples. The most abundant and speciose families were Diastylidae (26.9%; 13 species), Nannastacidae (23.2%; 19 species) and Leuconidae (26.3%; 7 species). Within these families the most speciose genus was *Campylaspis* (10 species), whereas *Leucon*, *Diastylis* and *Makrokilyndrus* presented similar number of species (4-5 species each). The most abundant species were *Diastyloides serratus*, *Leucon longirostris* and *Platysympus typicus* (Fig. 2.1.13).

Four species (*Campylaspis glabra*, *Cyclaspis longicaudata*, *Leptostylis macrura* and *Procampylaspis armata*) occurred throughout the studied bathymetric range (ca. 450-3000 m) and a high number of species (11 species e.g. *Diastyloides serratus*, *Procampylaspis bonnieri)* occurred from ca. 450 to 2250 m depth. Only four species (*Makrokylindrus josephinae, Iphinoe* cf. *serrata*, *Leucon mediterraneus*, *Diastylis richardi*) were found exclusively at depths shallower than 600 m while 13 species (e.g. *Platysympus typicus, Vaunthompsonia caeca*) were found exclusively at depths greater than 900 m (Fig. 2.1.14).

The high number of species found at deepest sites was probably related to the diminishing importance of other groups of peracarids with increasing depth in this region (Cartes and Sorbe, 1997). The investigated area presented the same dominant species as found in other Mediterranean areas, however this assemblage was more speciose, namely because of the high number of Nannastacidae species (19 species), thus contrasting with other Mediterranean areas characterized by a lesser representation of this family (12). This difference was probably related to the large bathymetric range studied and by the inclusion of regions characterized by increasing oligotrophic conditions. The predominance of Nannastacidae could be explained by their type of feeding (i.e. predators or scavengers), which may be more successful in the deep seafloor of oligotrophic areas (Corbera et al., 2009) such as studied herein. As with amphipods, their swimming behaviour has been assessed in the bathyal Mediterranean slopes by Cartes and Sorbe (1997) who demonstrated a high swimming behaviour for adults of the dominant species *L. longirostris* and *D. serratus.*

Figure 2.1.13 Specimens of cumaceans collected in the bathyal Mediterranean Sea. A: *Diastyloides serratus*, B: *Leucon longirostris*, C: *Platysympus typicus.*

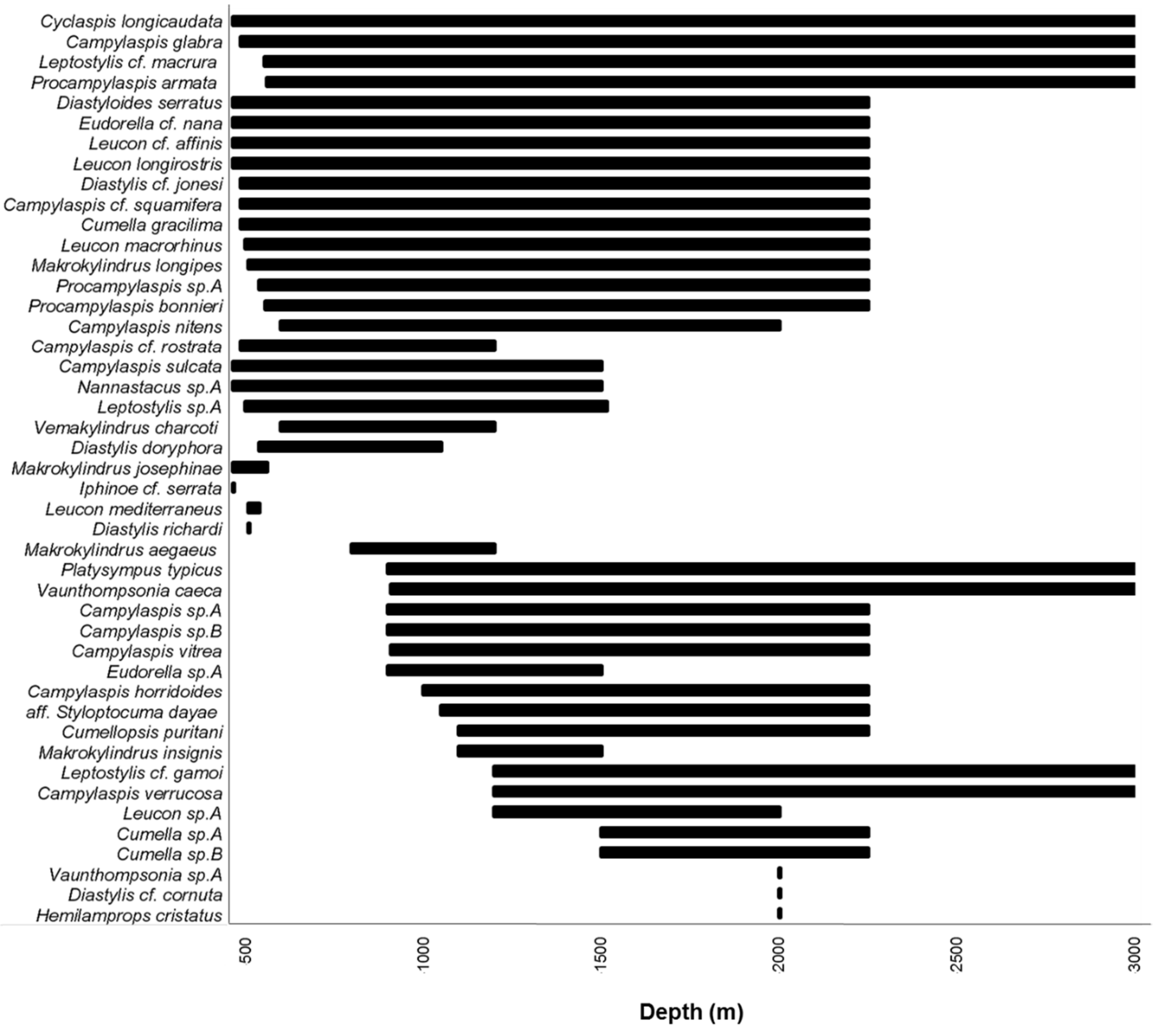

Figure 2.1.14 Bathymetric ranges of the cumacean species collected in the bathyal Mediterranean Sea. Undetermined specimens are not included.

Isopoda

Among the order **Isopoda**, eight families were identified tough most specimens belonged to a single taxon, the Munnopsidae (suborder Asellota), mainly Eurycopinae and Ilyarachninae (76% of the Isopoda sampled; 12 species), followed by Gnathiidae (12%). The most abundant species were *Munnopsurus atlanticus*, *Gnathiidae* sp.A and *Belonectes parvus* (Fig. 2.1.15).

Only three species (*Munnopsurus atlanticus*, *Ilyarachna* cf. *longicornis* and Gnathiidae sp.A) were collected in the entire bathymetric range (between 466 and 3000 m). Seven species (e.g. *Belonectes parvus*, *Disconectes phalangium*, *Chelator* sp.A) appeared in a large bathymetric range (ca. 500-2250 m) and twelve species appeared exclusively deeper than 900 m (e.g. *Ischnomesus bispinosus, Aegiochus incisa, Ilyarachna calidus*) (Fig. 2.1.16).

The isopods presented similar composition as found previously in the western Mediterranean slopes (Cartes et al., 2003). High abundance of the munnopsid *Munnopsurus atlanticus* was also described in the bathyal assemblages from the Mediterranean Sea (Cartes et al., 2000, 2003). Within its area of distribution (southeast Bay of Biscay, Portuguese upper slope, Catalan Sea and Levantine Sea) the depth ranged between 299 to 1859 m (Cartes et al., 2000 and references therein). This species was found in the entire bathymetric range studied (533-3000 m), despite its absence in Cap Ferret Canyon at 2400 m depth (Sorbe, 1999; Cartes et al., 2000).

Tanaidacea

The order **Tanaidacea** was very less represented (5 species) with few individuals of the sub-order Tanaidomorpha and Apseudomorpha occurring deeper than 800 m depth (Fig. 2.1.17). This group is mainly composed by infaunal species nevertheless, some species and "swimming males" are well adapted for a natatory lifestyle (Dauvin et al., 1995).

Figure 2.1.15 Specimens of isopods collected in the bathyal Mediterranean Sea. A: *Munnopsurus atlanticus*, B: Gnathiidae, C: *Belonectes parvus.*

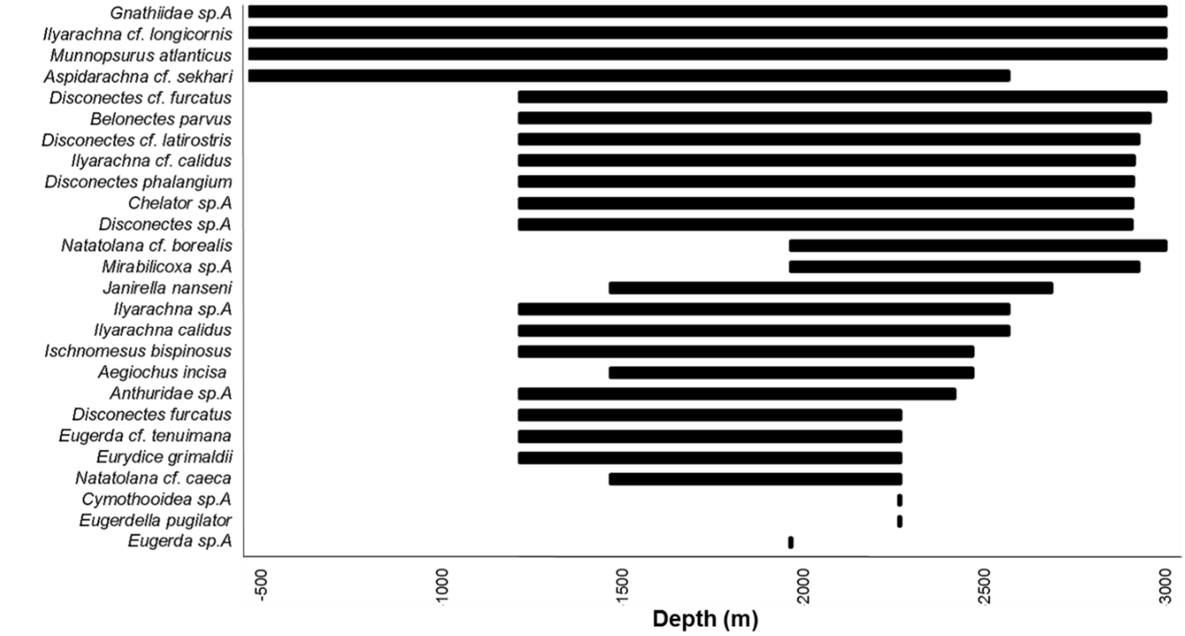

Figure 2.1.16 Bathymetric ranges of the isopod species collected in the bathyal Mediterranean Sea. Undetermined specimens are not included.

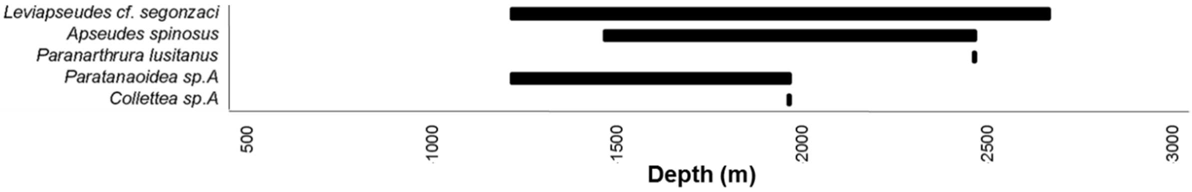

Figure 2.1.17 Bathymetric ranges of the tanaid species collected in the bathyal Mediterranean Sea. Undetermined specimens are not included.

Mysida and Lophogastrida

The order Lophogastrida was composed by only two pelagic species. Only one (*Eucopia unguicilata)* was collected throughout a wide bathymetric range (510-3000 m).

In relation to the order Mysida, the species *Boreomysis arctica* and *Hemimysis abyssicola*, represented more than 90% of the total specimens (Fig. 2.1.18). Mysids were most frequent at shallower depths. Only one species (*Boreomysis arctica*) was collected throughout the entire bathymetric range (466- 3000 m). Five species (e.g. *Paramblyops rostratus, Calyptomma puritani*) were found in a wide bathymetric range (ca. 400-2250 m) while four species (*Mysideis parva, Mysidella biscayensis, Boreomysis megalops, Haplostylus lobatus*) occurred exclusively shallower than 600 m. Seven species (e.g. *Erythrops neapolitanus, Pseudomma affine, Amblyops trisetosus*) were found exclusively shallower than 1200 m (Fig. 2.1.19).

Most of the mysids found in the Merenguera Canyon (Cartes and Sorbe, 1995) and Balearic slope (Cartes et al., 2003) were also components of the mysid fauna of the present work. These authors found some species confined to shallowest depths (<1000 m), a similar result observed in our study, however, an important difference emerged. High abundances of *Hemimysis abyssicola* was found in the Blanes Canyon shallower than 1500 m, while very few specimens were found in the Merenguera Canyon (Cartes and Sorbe, 1995) and few individuals of this genus were found in the Balearic Islands at deepest sites (Cartes et al., 2003). *Hemimysis abyssicola* is abundant in the Atlantic region and often dominate the assemblages (Cunha et al., 1997). This species may benefit of particular environmental conditions found in this canyon, as explained in Chapter 2.4.

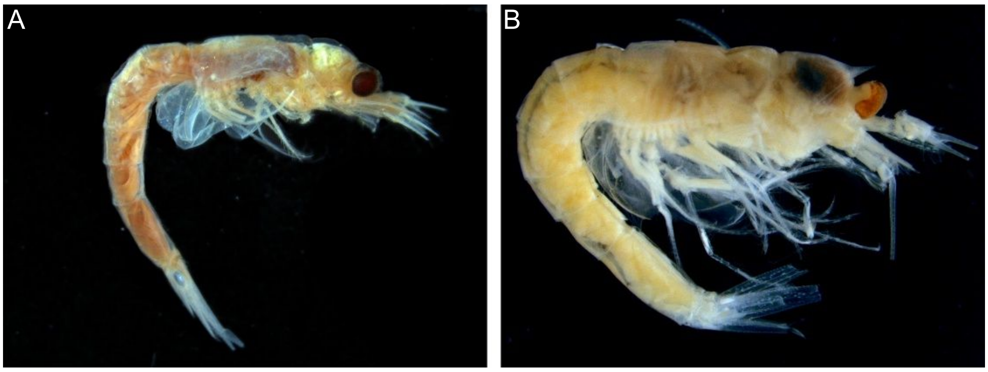

Figure 2.1.18 Specimens of mysids collected in the bathyal Mediterranean Sea. A: *Hemimysis abyssicola*, B: *Boreomysis arctica*.

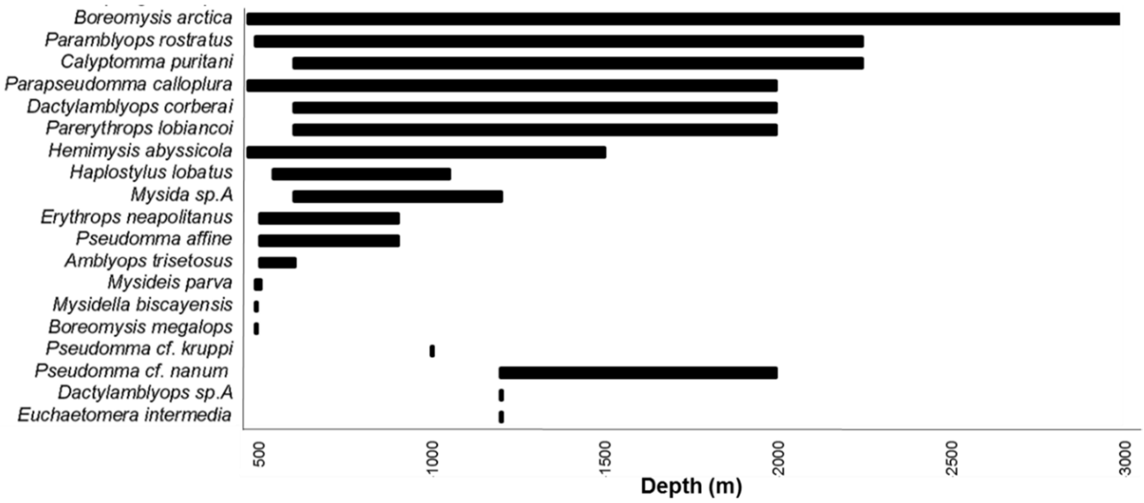

Figure 2.1.19 Bathymetric ranges of mysid species collected in the bathyal Mediterranean Sea. Undetermined specimens are not included.

Leptostraca

The order Leptostraca was very less represented with only one taxon found. The few individuals collected occurred deeper than 800 m.

Euphausiacea

This order was also of considerable importance given the numerical importance of some of the species collected. The most abundant species were *Nematoscelis megalops* and *Euphausia krohnii* (Fig. 2.1.20), the former representing 84% of the total abundance. Four species (*Euphausia krohnii, Euphausia hemigibba, Nematoscelis megalops* and *Stylocheiron longicorne*) were collected between 600 and 3000 m while five species (e.g. *Meganyctiphanes norvegica, Stylocheiron maximum*) occurred deeper than 900 m (Fig. 2.1.21). Euphausiids are found in the near-bottom environment, although they have a more temporally relationship with the seafloor, as they perform diel vertical migrations, some species with great amplitude of migrations such as *Euphausia krohni* while others, such as *Nemastocelis megalops* as a very patchy migration behaviour (Andersen and Sardou, 1992). In the Mediterranean Sea, *N. megalops* and *E. krohni* are dominant species (Cartes et al., 1994).

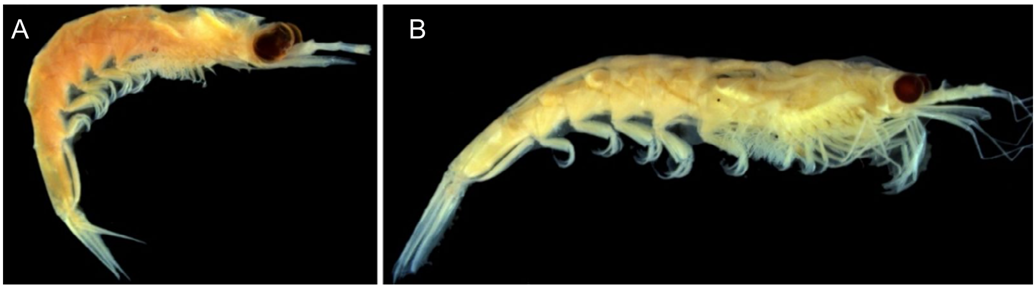

Figure 2.1.20 Specimens of euphausiids collected in the bathyal Mediterranean Sea. A: *Nemastocelis megalops*, B: *Euphausia krohnii*.

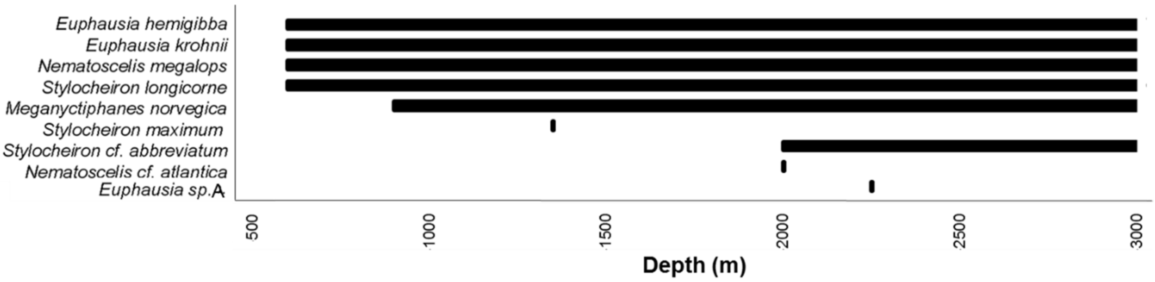

Figure 2.1.21 Bathymetric ranges of the euphausiid species collected in the bathyal Mediterranean Sea. Undetermined specimens were not included.

Decapoda

Despite quite speciose, the order **Decapoda** was mostly represented by few individuals, mostly shrimps. The most abundant species were *Acanthephyra eximia*, *Pontophilus norvegicus*, *Gennadas elegans*, *Calocaris macandreae*, *Aristeus antennatus* and *Nematocarcinus exilis* (Fig. 2.1.22). In general decapods showed wide bathymetric ranges with eight species occurring exclusively at depths greater than 1000 m (e.g. *Allosergestes sargassi*) (Fig. 2.1.23). In the deep Mediterranean Sea, high relative representability of decapods was found in comparison with the Atlantic Ocean (Cartes and Sardà, 1992) were other invertebrate groups, such as ophiuroids, predominate in megabenthic assemblages; it is hypothesised that decapods may be more resistant to the oligotrophic conditions of the Mediterranean Sea (Company et al., 2004).

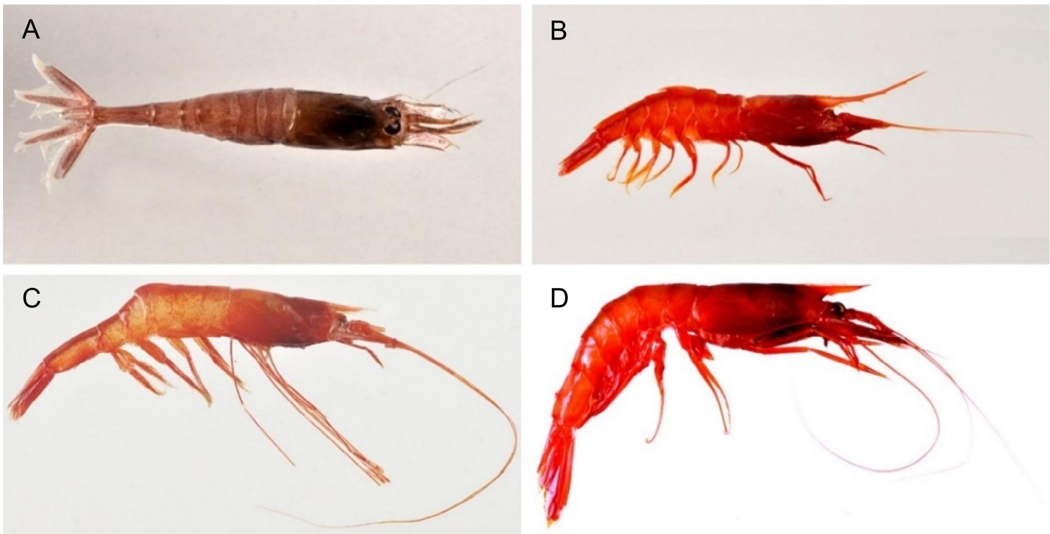

Figure 2.1.22 Specimens of decapods collected in the bathyal Mediterranean Sea. A: *Pontophylus norvegicus*, B: *Acanthephyra eximia*, C: *Nematocarcinus exilis*, D: *Aristeus antennatus*. (Photo credits Anna Bozanno).

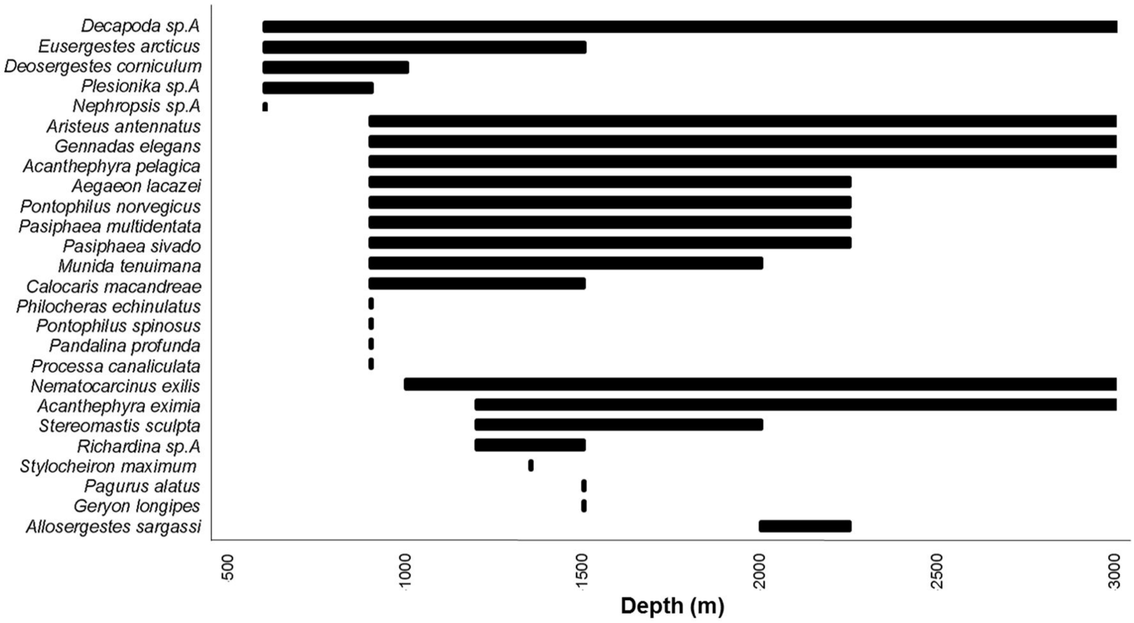

Figure 2.1.23 Bathymetric ranges of the decapod species collected in the bathyal Mediterranean Sea. Undetermined specimens are not included.

2.1.3.1 Constancy and fidelity

The assessment of the most characteristic taxa in the different regions and habitats (W, C and E; OS and BC) was made by using constancy (Const) and fidelity (Fidel) indices. Only the taxa with constancy ≥50 (constant, Const≥50) and fidelity ≥67 (exclusive, Fidel>90, and elective, 67<Fidel≤90) were considered. The taxa that were both abundant (top ten dominant species or with >1000 individuals) and constant were considered as the **baseline assemblage** (overall in the Mediterranean and for each basin or habitat) while constant taxa that were also elective or exclusive were considered as **distinctive taxa** of each basin or habitat (Table S 2.1.1, Supplementary material).

According to these criteria, several characteristic species were identified along the longitudinal gradient (W, C and E) (Figs. 2.1.24 and 2.1.25, Table S2.1.1, Supplementary material). A total of nine species were considered as the Trans-Mediterranean (TM) baseline assemblage, mostly represented by amphipods. The mysid *Boreomysis arctica*, the gammarid *Rhachotropis caeca* and the isopod *Munnopsurus atlanticus* were dominant species in the three regions; the euphausiid *Nematoscelis megalops* dominated in the West basin, the gammarids *Rhachotropis rostrata* and *Pseudotiron bouvieri* were dominant in the Central basin and *Mediterexis mimonectes* was dominant in the East basin*;* the other species were the amphipod *Ileraustroe ilergetes* and the euphausiid *Euphausia krohnii*.

From a total of 221 species found in the West basin, the baseline assemblage was formed by 31 species (nine TM; nine W and another 13 shared with one of the other basins), i.e. 18 gam/hyp amphipods, six cumaceans, three isopods, two euphausiids and two mysids/lophogastrids. The six distinctive species were the gammarids *Bathymedon acutifrons*, *B.banyulsensis*, *Monoculodes packardi* and *Syrrhoites* cf. *pusilla*, and the cumaceans *Leucon longirostris* and *Campylaspis* sp.B. A high number of trophic groups (10) formed the baseline assemblage in the West basin, mostly represented by predators on zooplankton and on meiofauna, omnivores and microbial grazers.

In the Central basin, from a total of 110 species collected, the baseline assemblage was formed by 33 species (nine TM, 10 C and another 14 shared with one of the other basins) from several groups: 11 gam/hyp amphipods, five isopods, seven cumaceans, four mysids, three decapods and three euphausiids. Only the decapod sp.A was classified as a distinctive species for this basin. Such as in the West basin, the central basin baseline assemblage, with 10 trophic groups, was in general represented by the same trophic groups as well as others with high mobility.

In the East basin, from a total of 67 species, the baseline assemblage was formed by 29 species (nine TM, 11 E and nine shared with one of the other basins) namely 15 gam/hyp amphipods, five euphausiids, three mysids/lophogastriids, two decapods, two isopods and two cumaceans. The hyperiids *Hyperiodes* sp.A, *Themisto* sp.A, *Ocycephalidae* sp.A and the euphausiid *Meganycthyphanes norvegica* were distinctive species. Epibenthic omnivores and predators on zooplankton were the most represented trophic groups.

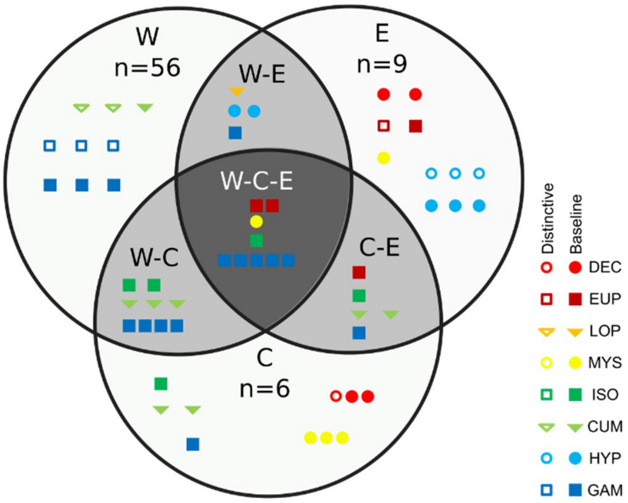

Figure 2.1.24 Baseline assemblage in each basin according to constancy and fidelity indices. W: western basin; C: central basin; E: eastern basin. n: number of samples.

The suprabenthic fauna in the Mediterranean Sea was characterized by swimmers often filterfeeding or hunting on prey, both in the water column and in the sediment. The presence of good swimmers could be associated to the oligotrophic conditions in several Mediterranean regions as motility can be advantageous in such conditions (Tselepsides et al., 2000; Corbera et al., 2009; Vicente et al., 2009).

In the West the presence of animals that forage in the sediment may reflect a high organic input to the sediments in comparison with more oligotrophic conditions in the East basin. The central basin, characterized by species with high mobility, could be associated to changing trophic conditions towards a more oligotrophic region. In the East, hyperiids and other groups characterized by high mobility and relying on food sources from the water column increased. These species may take advantage in this oligotrophic region of the Mediterranean Sea. As noted by Tselepides et al. (2000), motility, below a certain threshold of food availability, may became necessary to acquire sufficient food. The differences found between basins are probably related with the trophic gradient and the consequent availability of food supply to the seafloor, as shown by the changes in the trophic guilds.

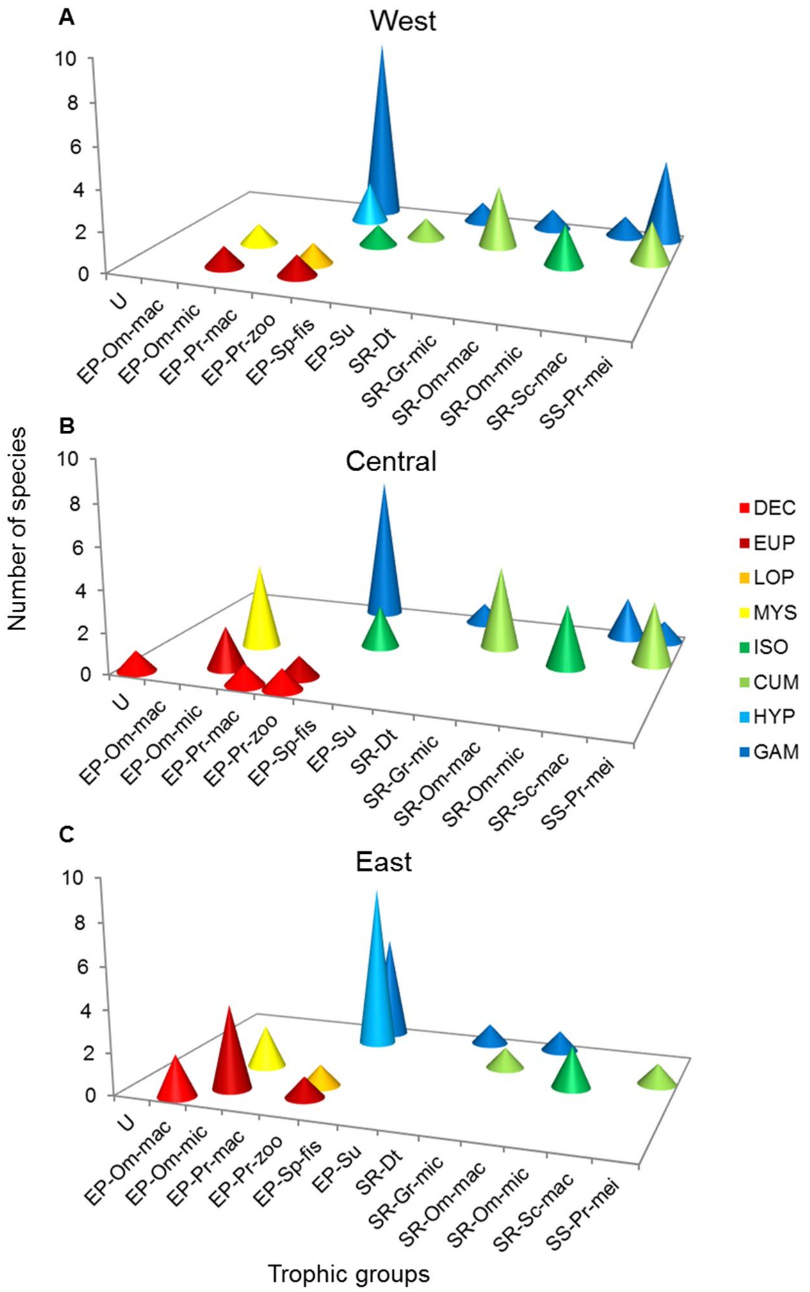

Figure 2.1.25 Characteristic taxa and trophic groups of the suprabenthic assemblages in each basin, according to constancy and fidelity indices.

In the West basin the characteristic species from the canyon and slope are summarised in Figures 2.1.26 and 2.1.27 (see also Table S2.1.2, Supplementary material). From a total of 221 species found in this basin (C: 177; OS:189), the baseline assemblage was formed by 22 species: 14 gam/hyp amphipods, three isopods, two euphausiids, two cumaceans and one mysid. Of these, several eusirids (*Rhachotropis* spp.), the mysid *Boreomysis arctica*, and the isopods *Munnopsurus atlanticus* and *Belonectes parvus* were among the dominant species in both environments; the cumacean *Diastyloides serratus a*nd the gammarid *Bathymedon acutifrons* were dominant in the canyon and the euphausiid *Nemastocelis megalops* and the amphipods *Mediterexis mimonectes*, *Ileraustroe ilergetes* and *Bathymedon longirostris* were dominant species in the open slope.

In the canyon, the baseline assemblage was formed by 35 species (22 BC-OS and 13 from the canyon) namely 21 gam/hyp amphipods, five isopods, four cumaceans, three mysids and two eupahusiids. The six distinctive species were the gam/hyp *Rhachotropis grimaldii, Scopelocheirus hopei*, *Synchelidium haplocheles and Primno macropa*, the mysid *Hemimysis abyssicola* and the isopod *Natatolana borealis.* The most representative trophic groups of the baseline assemblage were predators on zooplankton and on macro- and meiofauna, microbial grazers and epibenthic and surface omnivores.

In the open slope, the baseline assemblage was formed by 30 species (22 BC-OS and eight from the slope) namely 16 gam/hyp amphipods, six cumaceans, three mysids/lophogastrids, three isopods and two euphausiids. The cumaceans *Cyclaspis longicaudata*, *Makrokylindrus longipes* and *Vaunthompsonia caeca*, were classified as distinctive taxa for the slope assemblage. The most representative trophic groups of the baseline assemblage were predators on zooplankton and meiofauna, microbial grazers and epibenthic omnivores.

The relationship between food quantity and quality and the suprabenthic assemblages is also observed at a sub-basin scale when comparing the assemblage from the western Mediterranean open slopes and the ones from a submarine canyon. Here, the presence of several epibenthic omnivores and predators in the canyon and open slope assemblages may be explained by the trophic conditions associated to vertical and lateral inputs of organic matter to the deep-sea sediments as the result of the topography, closeness to coastal regions and localized more productive areas.

However, a high number of characteristic species and trophic groups was found in the canyon. These groups, that were found to reside at the sediment-water interface in the canyon, may benefit of the particular conditions found in this habitat, related to food enrichment in the sediment and the motility necessary to rapidly respond to food supply or escape from changing unfavourable conditions/disturbance events (Dewicke et al., 2002).

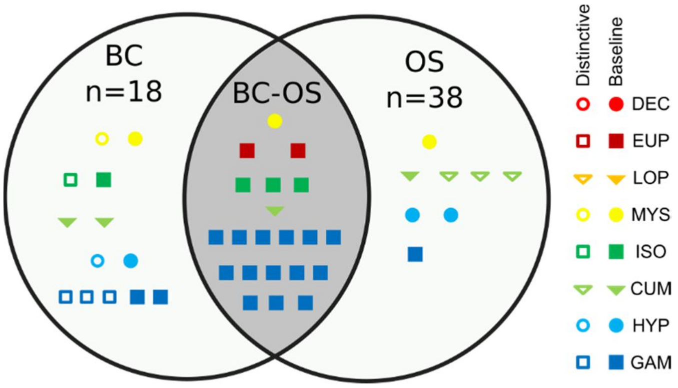

Figure 2.1.26 Baseline assemblage in each basin according to constancy and fidelity indices. BC: Blanes Canyon; OS: open slope. n: number of samples.

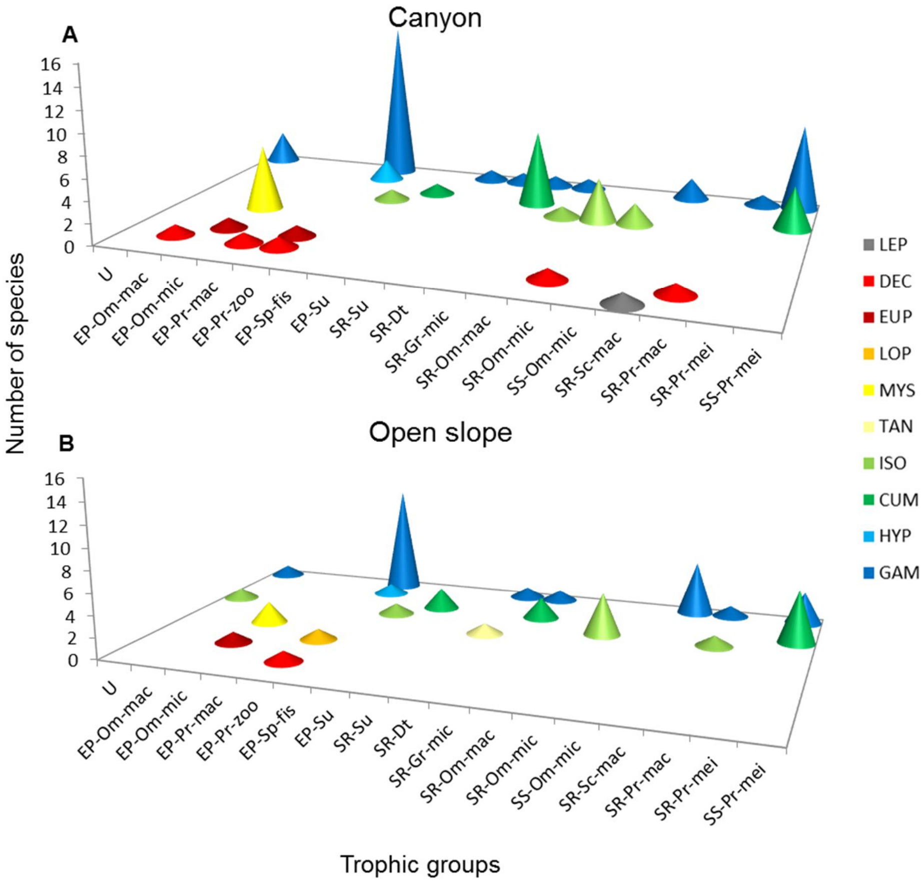

Figure 2.1.27 Characteristic taxa and trophic groups of the suprabenthic assemblages in each habitat, according to constancy and fidelity indices.

Supplementary material

Table S2.1.1 List of species and trophic guilds and the code corresponding to the characterization of the species based on fidelity (Fidel) and constancy (Const) indices in the three study regions.

Table S2.1.2 List of species and trophic guilds and the code corresponding to the characterization of the species based on fidelity (Fidel) and constancy (Const) indices in the two study habitats.

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Supplementary material

Table S2.1.1 List of species and trophic guilds and the code corresponding to the characterization of the species based on fidelity (Fidel) and constancy (Const) indices in the three study regions. Do: dominant (top ten species); Ab: abundant (>1000 ind.); Co: constant; Ae: accessory; Ai: accidental; Exc: exclusive; Ele: elective; Pre: preferential; Aco: accompanying; Rar: accidental or rare; SINGLET: occurrence only in one station. **Codes: BASE** (constant); **BASE D** (constant and elective or exclusive); **AE** (accessory and accompanying); **AE D** (accessory and elective or exclusive); **AE P** (accessory and preferential); **AI D** (accidental and elective or exclusive)**;** W: western region; C: central region; E: eastern region. TM: Trans-Mediterranean.

TG	Order	Species	West			Central			East			Code
			Abund	Const	Fidel	Abund	Const	Fidel	Abund	Const	Fidel	
		Trans-Mediterranean										
EP-Om-mic	MYS	*Boreomysis arctica*	Do	Co	Aco	Do	Co	Aco	Do	Co	Aco	**BASE TM**
EP-Om-mic	EUP	*Euphausia krohnii*	-	Co	Aco	-	Co	Aco	-	Co	Aco	BASE TM
EP-Pr-zoo	GAM	*Rhachotropis caeca*	Do	Co	Aco	Do	Co	Aco	Do	Co	Aco	**BASE TM**
EP-Pr-zoo	EUP	*Nematoscelis megalops*	Do	Co	Aco	-	Co	Aco	-	Co	Aco	BASE TM
EP-Pr-zoo	GAM	*Ileraustroe ilergetes*	Ab	Co	Aco	-	Co	Aco	-	Co	Aco	BASE TM
EP-Pr-zoo	GAM	*Rhachotropis rostrata*	-	Co	Aco	Do	Co	Aco	-	Co	Aco	BASE TM
EP-Pr-zoo	GAM	*Pseudotiron bouvieri*	-	Co	Aco	Do	Co	Aco	-	Co	Aco	BASE TM
SR-Dt	GAM	*Mediterexis mimonectes*	Ab	Co	Aco	-	Co	Aco	Do	Co	Aco	BASE TM
SR-Om-mic	ISO	*Munnopsurus atlanticus*	Do	Co	Aco	Do	Co	Aco	Do	Co	Aco	**BASE TM**
EP-Om-mic	MYS	*Dactylamblyops corberai*	-	Ae	Aco	-	Ae	Aco	-	Ae	Aco	AE TM
EP-Pr-zoo	GAM	*Syrrhoe* cf. *affinis*	-	Ae	Aco	-	Ae	Aco	-	Ae	Aco	AE TM
EP-Pr-zoo	HYP	*Scina* sp.A	-	Ae	Aco	-	Ae	Aco	-	Ae	Aco	AE TM
SR-Gr-mic	CUM	*Leptostylis* cf. *macrura*	-	Ae	Aco	-	Ae	Aco	-	Ae	Aco	AE TM
SR-Om-mac	ISO	*Natatolana* cf. *borealis*	-	Ae	Aco	-	Ae	Aco	-	Ae	Aco	AE TM
SR-Om-mic	ISO	*Disconectes* sp.A	-	Ae	Aco	-	Ae	Aco	Do	Ae	Aco	AE TM
SR-Pr-mac	AMP	*Stegocephaloides christianiensis*	-	Ae	Aco	-	Ae	Aco	-	Ae	Aco	AE TM

TG	Order	Species	West			Central			East			Code
			Abund	Const	Fidel	Abund	Const	Fidel	Abund	Const	Fidel	
SS-Pr-mei	CUM	*Campylaspis horridoides*	-	Ae	Aco	-	Ae	Aco	-	Ae	Aco	AE TM
		West-Center										
EP-Pr-zoo	GAM	*Rhachotropis glabra*	Do	Co	Aco	-	Co	Aco	-	Ae	Rar	BASE WC
EP-Pr-zoo	GAM	*Bruzelia typica*	Ab	Co	Aco	-	Co	Aco	-	Ae	Rar	BASE WC
EP-Sp-fis	ISO	Gnathiidae und.	Ab	Co	Pre	-	Co	Aco	-	Ae	Rar	BASE WC
SR-Gr-mic	CUM	*Diastyloides serratus*	Ab	Co	Aco	Do	Co	Aco	-	Ae	Aco	BASE WC
SR-Gr-mic	CUM	*Cyclaspis longicaudata*	-	Co	Aco	-	Co	Pre	-	-	-	BASE WC
SR-Om-mic	ISO	*Belonectes parvus*	Ab	Co	Pre	-	Co	Aco	-	-	-	BASE WC
SR-Sc-mac	GAM	*Tryphosa nana*	-	Co	Pre	-	Co	Aco	-	-	-	BASE WC
SS-Pr-mei	GAM	*Bathymedon longirostris*	Do	Co	Pre	-	Co	Aco	-	-	-	BASE WC
SS-Pr-mei	CUM	*Procampylaspis bonnieri*	-	Co	Aco	-	Co	Pre	-	-	-	BASE WC
		Center -East										
EP-Om-mic	EUP	*Euphausia hemigibba*	-	-	-	-	Co	Aco	Do	Co	Pre	BASE CE
EP-Pr-zoo	GAM	*Epimeria cornigera*	-	Ae	Rar	Do	Co	Pre	-	Co	Aco	BASE CE
SR-Gr-mic	CUM	*Platysympus typicus*	-	Ae	Rar	Do	Co	Aco	Do	Co	Aco	BASE CE
SR-Om-mic	ISO	*Ilyarachna* cf. *longicornis*	-	Ae	Aco	Do	Co	Aco	-	Co	Aco	BASE CE
SS-Pr-mei	CUM	*Procampylaspis armata*	-	Ae	Aco	-	Co	Aco	-	Co	Aco	BASE CE
SR-Om-mic	ISO	*Disconectes phalangium*	-	Ae	Rar	-	Ae	Aco	-	Ae	Aco	AE CE
EP-Pr-mac	DEC	*Acanthephyra pelagica*	-	Ae	Rar	-	Ae	Aco	-	Ae	Aco	AE CE
		West-East										
EP-Pr-zoo	HYP	*Hyperiia* spp.	-	Co	Aco	-	Ae	Aco	-	Co	Aco	BASE WE
EP-Pr-zoo	LOP	*Eucopia unguiculata*	-	Co	Aco	-	Ae	Aco	-	Co	Aco	BASE WE
EP-Pr-zoo	HYP	*Vibilia armata*	-	Co	Aco	-	Ae	Rar	-	Co	Aco	BASE WE
SR-Om-mac	GAM	*Scopelocheirus hopei*	Do	Co	Aco	-	Ae	Aco	-	Co	Aco	BASE WE

TG	Order	Species	West			Central			East			Code
			Abund	Const	Fidel	Abund	Const	Fidel	Abund	Const	Fidel	
		West basin										
EP-Pr-zoo	GAM	*Syrrhoites* cf. *pusilla*	-	Co	Ele	-	Ae	Aco	-	-	-	BASE D W
SR-Gr-mic	CUM	*Leucon longirostris*	Ab	Co	Ele	-	Ae	Rar	-	-	-	BASE D W
SS-Pr-mei	GAM	*Bathymedon acutifrons*	Do	Co	Exc	-	-	-	-	-	-	BASE D W
SS-Pr-mei	GAM	*Bathymedon banyulsensis*	Ab	Co	Exc	-	-	-	-	-	-	BASE D W
SS-Pr-mei	CUM	*Campylaspis* sp.B	-	Co	Exc	-	-	-	-	-	-	BASE D W
SS-Pr-mei	GAM	*Monoculodes packardi*	-	Co	Exc	-	-	-	-	-	-	BASE D W
EP-Pr-zoo	GAM	*Eusirus longipes*	-	Co	Pre	-	-	-	-	Ae	Aco	BASE W
EP-Pr-zoo	GAM	*Halice abyssi*	-	Co	Pre	-	Ae	Rar	-	Ae	Aco	BASE W
EP-Su	CUM	*Makrokylindrus longipes*	-	Co	Aco	-	Ae	Aco	-	Ae	Aco	BASE W
EP-Om-mic	MYS	*Hemimysis abyssicola*	Do	Ae	Exc	-	-	-	-	-	-	AE D W
EP-Om-mic	MYS	*Pseudomma affine*	-	Ae	Exc	-	-	-	-	-	-	AE D W
EP-Pr-zoo	GAM	*Rhachotropis integricauda*	-	Ae	Exc	-	-	-	-	-	-	AE D W
EP-Pr-zoo	GAM	*Pardalisca mediterranea*	-	Ae	Exc	-	-	-	-	-	-	AE D W
EP-Pr-zoo	GAM	*Eusirus leptocarpus*	-	Ae	Exc	-	-	-	-	-	-	AE D W
EP-Pr-zoo	GAM	*Arculfia trago*	-	Ae	Exc	-	-	-	-	-	-	AE D W
EP-Pr-zoo	GAM	*Syrrhoe angulipes*	-	Ae	Exc	-	-	-	-	-	-	AE D W
EP-Pr-zoo	DEC	*Pasiphaea multidentata*	-	Ae	Exc	-	-	-	-	-	-	AE D W
EP-Su	GAM	*Leucothoe lilljeborgi*	-	Ae	Ele	-	Ae	Aco	-	-	-	AE D W
SR-Dt	ISO	*Ischnomesus bispinosus*	-	Ae	Exc	-	-	-	-	-	-	AE D W
SR-Dt	ISO	*Janirella nanseni*	-	Ae	Exc	-	-	-	-	-	-	AE D W
SR-Dt	TAN	*Leviapseudes* cf. *segonzaci*	-	Ae	Exc	-	-	-	-	-	-	AE D W
SR-Gr	GAM	*Seba aloe*	-	Ae	Exc	-	-	-	-	-	-	AE D W
SR-Gr-mic	CUM	*Leucon macrorhinus*	-	Ae	Ele	-	Ae	Aco	-	-	-	AE D W
SR-Gr-mic	CUM	*Eudorella* cf. *nana*	-	Ae	Exc	-	-	-	-	-	-	AE D W
SR-Gr-mic	CUM	*Diastylis* cf. *jonesi*	-	Ae	Exc	-	-	-	-	-	-	AE D W

TG	**Order**	**Species**	**West**			**Central**			**East**			**Code**
			Abund	Const	Fidel	Abund	Const	Fidel	Abund	Const	Fidel	
SR-Om-mic	ISO	*Disconectes* cf. *latirostris*	-	Ae	Exc	-	-	-	-	-	-	AE D W
SR-Om-mic	ISO	*AspidarAEhna* cf. *sekhari*	-	Ae	Ele	-	Ae	Aco	-	-	-	AE D W
SR-Om-mic	ISO	*Ilyarachna* cf. *calidus*	-	Ae	Exc	-	-	-	-	-	-	AE D W
SR-Pr-mac	DEC	*Pontophilus norvegicus*	-	Ae	Ele	-	Ae	Aco	-	-	-	AE D W
SR-Pr-mac	DEC	*Aegaeon lacazei*	-	Ae	Exc	-	-	-	-	-	-	AE D W
SR-Pr-mei	GAM	*Harpinia dellavallei*	-	Ae	Exc	-	-	-	-	-	-	AE D W
SR-Sc-mac	GAM	*Caeconyx caeculus*	-	Ae	Ele	-	Ae	Aco	-	-	-	AE D W
SR-Sc-mac	GAM	*Lepidepecreum subclypeatum*	-	Ae	Exc	-	-	-	-	-	-	AE D W
SR-Sc-mac	GAM	*Paracentromedon crenulatus*	-	Ae	Exc	-	-	-	-	-	-	AE D W
SR-Sc-mac	GAM	*Tryphosella longidactyla*	-	Ae	Exc	-	-	-	-	-	-	AE D W
SR-Sc-mac	GAM	cf. *Podoprion sp.A*	-	Ae	Exc	-	-	-	-	-	-	AE D W
SS-Om-mic	ISO	*Eugerda* cf. *tenuimana*	-	Ae	Exc	-	-	-	-	-	-	AE D W
SS-Pr-mei	GAM	*Synchelidium haplocheles*	Do	Ae	Exc	-	-	-	-	-	-	AE D W
SS-Pr-mei	GAM	*Oediceropsis brevicornis*	-	Ae	Exc	-	-	-	-	-	-	AE D W
SS-Pr-mei	GAM	*Westwoodilla caecula*	-	Ae	Exc	-	-	-	-	-	-	AE D W
SS-Pr-mei	GAM	*Arrhis mediterraneus*	-	Ae	Ele	-	Ae	Aco	-	-	-	AE D W
SS-Pr-mei	CUM	*Campylaspis* cf. *squamifera*	-	Ae	Exc	-	-	-	-	-	-	AE D W
SS-Pr-mei	CUM	*Procampylaspis* sp.A	-	Ae	Exc	-	-	-	-	-	-	AE D W
SS-Pr-mei	CUM	*Campylaspis sulcata*	-	Ae	Exc	-	-	-	-	-	-	AE D W
SS-Pr-mei	GAM	*Monoculodes* sp.A	-	Ae	Exc	-	-	-	-	-	-	AE D W
SS-Pr-mei	CUM	*Cumellopsis puritani*	-	Ae	Exc	-	-	-	-	-	-	AE D W
SS-Pr-mei	GAM	*Bathymedon* cf. *monoculodiformis*	-	Ae	Exc	-	-	-	-	-	-	AE D W
SS-Pr-mei	CUM	*Cumella* sp.A	-	Ae	Exc	-	-	-	-	-	-	AE D W
SS-Pr-mei	CUM	*Nannastacus* sp.A	-	Ae	Exc	-	-	-	-	-	-	AE D W
EP-Pr-zoo	GAM	*Rhachotropis grimaldii*	-	Ae	Pre	-	Ae	Aco	-	-	-	AE P W
SR-Gr-mic	CUM	*Leucon* cf. *affinis*	-	Ae	Pre	-	Ae	Aco	-	-	-	AE P W
SR-Gr-mic	CUM	*Leptostylis* sp.A	-	Ae	Pre	-	Ae	Aco	-	-	-	AE P W

TG	Order	Species	West			Central			East			Code
			Abund	Const	Fidel	Abund	Const	Fidel	Abund	Const	Fidel	
SR-Om-mic	ISO	*Disconectes* cf. *furcatus*	-	Ae	Pre	-	Ae	Aco	-	-	-	AE P W
SR-Sc-mac	GAM	*Tryphosites alleni*	-	Ae	Pre	-	Ae	Aco	-	-	-	AE P W
SR-Sc-mac	LEP	Leptostraca sp.A	-	Ae	Pre	-	Ae	Aco	-	-	-	AE P W
SS-De	DEC	*Calocaris macandreae*	-	Ae	Pre	-	Ae	Aco	-	-	-	AE P W
SS-Om-mic	ISO	*Chelator* sp.A	-	Ae	Pre	-	Ae	Aco	-	-	-	AE P W
SS-Pr-mei	CUM	*Campylaspis vitrea*	-	Ae	Pre	-	Ae	Aco	-	-	-	AE P W
SS-Pr-mei	CUM	*Cumella gracilima*	-	Ae	Pre	-	Ae	Aco	-	-	-	AE P W
U	GAM	*Carangoliopsis spinulosa*	-	Ae	Pre	-	Ae	Aco	-	-	-	AE P W
U	GAM	*Lepechinella manco*	-	Ae	Pre	-	Ae	Aco	-	-	-	AE P W
EP-Om	DEC	*Eusergestes arcticus*	-	Ai	Exc	-	-	-	-	-	-	AI D W
EP-Om	DEC	*Allosergestes sargassi*	-	Ai	Exc	-	-	-	-	-	-	AI D W
EP-Om-mic	MYS	*Amblyops trisetosus*	-	Ai	Exc	-	-	-	-	-	-	AI D W
EP-Om-mic	MYS	*Mysidella biscayensis*	-	Ai	Exc	-	-	-	-	-	-	AI D W
EP-Om-mic	MYS	*Mysideis parva*	-	Ai	Exc	-	-	-	-	-	-	AI D W
EP-Pr-zoo	HYP	*Phronima sedentaria*	-	Ai	Exc	-	-	-	-	-	-	AI D W
EP-Pr-zoo	DEC	*Processa canaliculata*	-	Ai	Exc	-	-	-	-	-	-	AI D W
EP-Pr-zoo	AMP	*Syrrhoites* cf. *cornuta*	-	Ai	Exc	-	-	-	-	-	-	AI D W
EP-Su	CUM	*Makrokylindrus insignis*	-	Ai	Exc	-	-	-	-	-	-	AI D W
EP-Su	CUM	*Makrokylindrus josephinae*	-	Ai	Exc	-	-	-	-	-	-	AI D W
EP-Su	CUM	*Makrokylindrus aegaeus*	-	Ai	Exc	-	-	-	-	-	-	AI D W
SR-Dt	TAN	Paratanaoidea sp.A	-	Ai	Exc	-	-	-	-	-	-	AI D W
SR-Dt	TAN	*Apseudes spinosus*	-	Ai	Exc	-	-	-	-	-	-	AI D W
SR-Gr-mic	CUM	*Eudorella* sp.A	-	Ai	Exc	-	-	-	-	-	-	AI D W
SR-Gr-mic	CUM	*Leucon mediterraneus*	-	Ai	Exc	-	-	-	-	-	-	AI D W
SR-Gr-mic	SEN	*Parvipalpus major*	-	Ai	Exc	-	-	-	-	-	-	AI D W
SR-Om-mac	ISO	*Natatolana* cf. *caeca*	-	Ai	Exc	-	-	-	-	-	-	AI D W
SR-Om-mac	DEC	*Munida tenuimana*	-	Ai	Exc	-	-	-	-	-	-	AI D W

TG	**Order**	**Species**	**West**			**Central**			**East**			**Code**
			Abund	Const	Fidel	Abund	Const	Fidel	Abund	Const	Fidel	
SR-Om-mic	ISO	*Disconectes furcatus*	-	Ai	Exc	-	-	-	-	-	-	AI D W
SR-Om-mic	ISO	*Ilyarachna* sp.A	-	Ai	Exc	-	-	-	-	-	-	AI D W
SR-Om-mic	DEC	*Richardina* sp.A	-	Ai	Exc	-	-	-	-	-	-	AI D W
SR-Pr-mac	ISO	*Eurydice grimaldii*	-	Ai	Exc	-	-	-	-	-	-	AI D W
SR-Sc-mac	GAM	*Tryphosella simillima*	-	Ai	Exc	-	-	-	-	-	-	AI D W
SR-Sc-mac	GAM	*Sophrosyne hispana*	-	Ai	Exc	-	-	-	-	-	-	AI D W
SR-Sc-mac	GAM	*Sophrosyne* sp.A	-	Ai	Exc	-	-	-	-	-	-	AI D W
SR-Su	SEN	Aoridae sp.A	-	Ai	Exc	-	-	-	-	-	-	AI D W
SR-Su	GAM	*Ampelisca cf diadema*	-	Ai	Exc	-	-	-	-	-	-	AI D W
SR-Su	GAM	cf. *Byblis* sp.A	-	Ai	Exc	-	-	-	-	-	-	AI D W
SR-Su	GAM	*Lembos* sp.A	-	Ai	Exc	-	-	-	-	-	-	AI D W
SS-Om-mic	ISO	*Eugerda* sp.A	-	Ai	Exc	-	-	-	-	-	-	AI D W
SS-Om-mic	ISO	*Mirabilicoxa* sp.A	-	Ai	Exc	-	-	-	-	-	-	AI D W
SS-Pr-mei	GAM	*Perioculodes longimanus*	-	Ai	Exc	-	-	-	-	-	-	AI D W
SS-Pr-mei	GAM	*Deflexilodes griseus*	-	Ai	Exc	-	-	-	-	-	-	AI D W
SS-Pr-mei	GAM	*Deflexilodes acutipes*	-	Ai	Exc	-	-	-	-	-	-	AI D W
SS-Pr-mei	GAM	*Monoculodes* cf. *latissimanus*	-	Ai	Exc	-	-	-	-	-	-	AI D W
SS-Pr-mei	CUM	aff. *Styloptocuma dayae*	-	Ai	Exc	-	-	-	-	-	-	AI D W
SS-Pr-mei	CUM	*Campylaspis verrucosa*	-	Ai	Exc	-	-	-	-	-	-	AI D W
SS-Pr-mei	CUM	*Campylaspis* sp.A	-	Ai	Exc	-	-	-	-	-	-	AI D W
SS-Pr-mei	CUM	*Cumella* sp.B	-	Ai	Exc	-	-	-	-	-	-	AI D W
U	GAM	*Amphilochoides serratipes*	-	Ai	Exc	-	-	-	-	-	-	AI D W
U	ISO	Anthuridae sp.A	-	Ai	Exc	-	-	-	-	-	-	AI D W
U	GAM	*Amphilochus planieriensis*	-	Ai	Exc	-	-	-	-	-	-	AI D W
		Central basin										
U	DEC	Decapoda sp.A	-	Ai	Rar	-	Co	Exc	-	-	-	BASE D C

TG	Order	Species	West			Central			East			Code
			Abund	Const	Fidel	Abund	Const	Fidel	Abund	Const	Fidel	
EP-Om-mic	MYS	*Calyptomma puritani*	-	Ae	Aco	Do	Co	Aco	Do	Ae	Aco	BASE C
EP-Om-mic	MYS	*Parerythrops lobiancoi*	-	Ai	Rar	-	Co	Pre	Do	Ae	Aco	BASE C
EP-Om-mic	MYS	*Parapseudomma calloplura*	-	Ae	Aco	-	Co	Aco	-	Ae	Aco	BASE C
EP-Pr-mac	DEC	*Acanthephyra eximia*	-	Ae	Aco	-	Co	Pre	-	Ae	Aco	BASE C
EP-Pr-zoo	DEC	*Nematocarcinus exilis*	-	Ae	Rar	-	Co	Pre	-	Ae	Aco	BASE C
EP-Sp-fis	ISO	*Aegiochus incisa*	-	Ai	Rar	-	Co	Pre	-	Ae	Aco	BASE C
SR-Gr-mic	CUM	*Vaunthompsonia caeca*	-	Ae	Aco	-	Co	Aco	-	Ae	Aco	BASE C
SR-Sc-mac	GAM	*Orchomene grimaldi*	-	Ae	Rar	-	Co	Pre	-	Ae	Aco	BASE C
SS-Pr-mei	CUM	*Campylaspis glabra*	-	Ae	Aco	-	Co	Aco	-	Ae	Aco	BASE C
EP-Om	DEC	*Deosergestes corniculum*	-	-	-	-	Ae	Exc	-	-	-	AE D C
EP-Om-mic	MYS	Mysida sp.A	-	Ai	Rar	-	Ae	Ele	-	-	-	AE D C
EP-Om-mic	EUP	*Stylocheiron* cf. *abbreviatum*	-	Ai	Rar	-	Ae	Exc	-	-	-	AE D C
EP-Pr-zoo	DEC	*Pasiphaea sivado*	-	Ai	Aco	-	Ae	Ele	-	-	-	AE D C
EP-Pr-zoo	DEC	*Plesionika* sp.A	-	Ai	Rar	-	Ae	Exc	-	-	-	AE D C
EP-Pr-zoo	AMP	Lycaeidae sp.A	-	Ai	Rar	-	Ae	Exc	-	-	-	AE D C
EP-Su	GAM	*Leucothoe incisa*	-	Ai	Rar	-	Ae	Exc	-	-	-	AE D C
SR-Gr-mic	CUM	*Vemakylindrus charcoti*	-	Ai	Rar	-	Ae	Exc	-	-	-	AE D C
SR-Gr-mic	CUM	*Leucon* sp.A	-	Ai	Rar	-	Ae	Ele	-	-	-	AE D C
SR-Om-mac	DEC	*Stereomastis sculpta*	-	Ai	Rar	-	Ae	Exc	-	-	-	AE D C
SR-Sc-mac	GAM	*Lysianassa plumosa*	-	Ai	Rar	-	Ae	Exc	-	-	-	AE D C
SR-Sc-mac	GAM	*Tmetonyx similis*	-	Ae	Aco	-	Ae	Ele	-	-	-	AE D C
SR-Sc-mac	GAM	*Normanion ruffoi*	-	Ai	Rar	-	Ae	Ele	-	-	-	AE D C
SR-Sc-mac	GAM	*Hippomedon bidentatus*	-	Ai	Rar	-	Ae	Exc	-	-	-	AE D C
SS-Pr-mei	CUM	*Campylaspis nitens*	-	Ai	Rar	-	Ae	Exc	-	-	-	AE D C
EP-Om-mic	MYS	*Erythrops neapolitanus*	-	Ae	Aco	-	Ae	Pre	-	-	-	AE P C
EP-Pr-zoo	GAM	*Nicippe tumida*	-	Ae	Aco	-	Ae	Pre	-	-	-	AE P C

TG	Order	Species	West			Central			East			Code
			Abund	Const	Fidel	Abund	Const	Fidel	Abund	Const	Fidel	
EP-Pr-zoo	GAM	*Halice walkeri*	-	Ae	Aco	-	Ae	Pre	-	-	-	AE P C
SR-Gr-mic	CUM	*Diastylis doryphora*	-	Ae	Aco	-	Ae	Pre	-	-	-	AE P C
SR-Om-mic	ISO	*Ilyarachna calidus*	-	Ae	Aco	-	Ae	Pre	-	-	-	AE P C
SR-Pr-mei	GAM	*Harpinia truncata*	-	Ai	Aco	-	Ae	Pre	-	-	-	AE P C
SR-Pr-mei	GAM	*Metaphoxus simplex*	-	Ai	Aco	-	Ae	Pre	-	-	-	AE P C
SS-Pr-mei	GAM	*Oediceroides pilosa*	-	Ae	Aco	-	Ae	Pre	-	-	-	AE P C
U	GAM	*Idunella pirata*	-	Ae	Aco	-	Ae	Pre	-	-	-	AE P C
		East basin										
EP-Om-mic	EUP	*Meganyctiphanes norvegica*	-	Ae	Rar	-	Ae	Rar	-	Co	Ele	BASE D E
EP-Pr-zoo	HYP	*Hyperioides* sp.A	-	Ai	Rar	-	Ae	Aco	Do	Co	Ele	BASE D E
EP-Pr-zoo	HYP	*Themisto* sp.A	-	-	-	-	-	-	-	Co	Exc	BASE D E
EP-Pr-zoo	HYP	Ocycephalidae sp.A	-	Ai	Rar	-	Ae	Rar	-	Co	Ele	BASE D E
EP-Om-mac	DEC	*Aristeus antennatus*	-	Ae	Rar	-	Ae	Aco	-	Co	Pre	BASE E
EP-Om-mac	DEC	*Gennadas elegans*	-	Ae	Aco	-	Ae	Rar	-	Co	Pre	BASE E
EP-Om-mic	MYS	*Paramblyops rostratus*	-	Ae	Aco	-	Ae	Aco	-	Co	Aco	BASE E
EP-Om-mic	EUP	*Stylocheiron longicorne*	-	Ae	Rar	-	Ae	Aco	-	Co	Pre	BASE E
EP-Pr-zoo	HYP	*Primno macropa*	-	Ae	Aco	-	Ae	Rar	-	Co	Pre	BASE E
EP-Pr-zoo	HYP	*Hyperioides longipes*	-	-	-	-	Ae	Aco	-	Co	Pre	BASE E
EP-Pr-zoo	HYP	*Phrosina semilunata*	-	Ae	Rar	-	Ae	Aco	-	Co	Pre	BASE E
EP-Om-mic	MYS	*Pseudomma* cf. *nanum*	-	Ai	Rar	-	-	-	-	Ae	Exc	AE D E
SS-Pr-mei	CUM	*Campylaspis* cf. *rostrata*	-	Ai	Rar	-	-	-	-	Ae	Exc	AE D E
EP-Pr-zoo	GAM	*Anchylomera blossevillei*	-	-	-	-	Ae	Aco	-	Ae	Pre	AE P E
EP-Pr-zoo	GAM	*Epimeria parasitica*	-	-	-	-	Ae	Aco	-	Ae	Pre	AE P E
EP-Pr-zoo	AMP	*Phronima atlantica*	-	Ai	Rar	-	Ae	Aco	-	Ae	Pre	AE P E

TG	Order	Species	West			Central			East			Code
			Abund	Const	Fidel	Abund	Const	Fidel	Abund	Const	Fidel	
SR-Gr-mic	CUM	*Leptostylis* cf. *gamoi*	-	Ai	Rar	-	Ae	Aco	-	Ae	Pre	AE P E
SR-Sc-mac	GAM	*Tryphosella* cf. *nanoides*	-	Ae	Aco	-	Ae	Aco	-	Ae	Pre	AE P E
SR-Sc-mac	GAM	*Tryphosites longipes*	-	Ae	Aco	-	Ae	Aco	-	Ae	Pre	AE P E
		Singletons										
Ep-Om	DEC	cf. *Sergia robusta*	-	Ai	Exc	-	-	-	-	-	-	SINGLET W
EP-Om-mic	MYS	*Haplostylus lobatus*	-	Ai	Exc	-	-	-	-	-	-	SINGLET W
EP-Om-mic	EUP	*Euphausia* sp.A	-	Ai	Exc	-	-	-	-	-	-	SINGLET W
EP-Om-mic	MYS	*Boreomysis megalops*	-	Ai	Exc	-	-	-	-	-	-	SINGLET W
EP-Om-mic	MYS	*Dactylamblyops* sp.A	-	Ai	Exc	-	-	-	-	-	-	SINGLET W
EP-Om-mic	EUP	*Nematoscelis* cf. *atlantica*	-	Ai	Exc	-	-	-	-	-	-	SINGLET W
EP-Om-mic	EUP	*Stylocheiron maximum*	-	Ai	Exc	-	-	-	-	-	-	SINGLET W
EP-Pr-zoo	GAM	Eusiridae sp.A	-	Ai	Exc	-	-	-	-	-	-	SINGLET W
EP-Pr-zoo	GAM	*Pardalisca brachydactyla*	-	Ai	Exc	-	-	-	-	-	-	SINGLET W
EP-Pr-zoo	DEC	*Pandalina profunda*	-	Ai	Exc	-	-	-	-	-	-	SINGLET W
Ep-Pr-zoo	LOP	cf. *Lophogaster* sp.A	-	Ai	Exc	-	-	-	-	-	-	SINGLET W
EP-Sp-fis	ISO	*Cymothoida* sp.A	-	Ai	Exc	-	-	-	-	-	-	SINGLET W
EP-Su	GAM	*Melphidippella macra*	-	Ai	Exc	-	-	-	-	-	-	SINGLET W
SR-Dt	TAN	*Paranarthrura lusitanus*	-	Ai	Exc	-	-	-	-	-	-	SINGLET W
SR-Dt	SEN	*Psammogammarus caecus*	-	Ai	Exc	-	-	-	-	-	-	SINGLET W
SR-Dt	TAN	*Collettea* sp.A	-	Ai	Exc	-	-	-	-	-	-	SINGLET W
SR-Gr-mic	CUM	*Iphinoe* cf. *serrata*	-	Ai	Exc	-	-	-	-	-	-	SINGLET W
SR-Gr-mic	CUM	*Diastylis richardi*	-	Ai	Exc	-	-	-	-	-	-	SINGLET W
SR-Gr-mic	CUM	*Vaunthompsonia* sp.A	-	Ai	Exc	-	-	-	-	-	-	SINGLET W
SR-Gr-mic	CUM	*Diastylis* cf. *cornuta*	-	Ai	Exc	-	-	-	-	-	-	SINGLET W
SR-Gr-mic	CUM	*Hemilamprops cristatus*	-	Ai	Exc	-	-	-	-	-	-	SINGLET W
SR-Om-mac	DEC	*Nephropsis* sp.A	-	Ai	Exc	-	-	-	-	-	-	SINGLET W
SR-Om-mac	DEC	*Pagurus alatus*	-	Ai	Exc	-	-	-	-	-	-	SINGLET W

TG	**Order**	**Species**	**West**			**Central**			**East**			**Code**
			Abund	Const	Fidel	Abund	Const	Fidel	Abund	Const	Fidel	
SR-Om-mac	DEC	*Geryon longipes*	-	Ai	Exc	-	-	-	-	-	-	SINGLET W
SR-Pr-mac	GAM	*Iphimedia* sp.A	-	Ai	Exc	-	-	-	-	-	-	SINGLET W
SR-Pr-mac	DEC	*Philocheras echinulatus*	-	Ai	Exc	-	-	-	-	-	-	SINGLET W
SR-Pr-mac	DEC	*Pontophilus spinosus*	-	Ai	Exc	-	-	-	-	-	-	SINGLET W
SR-Sc-mac	GAM	*Orchomene* cf. *massiliensis*	-	Ai	Exc	-	-	-	-	-	-	SINGLET W
SR-Sc-mac	GAM	*Tmetonyx* cf. *dilatata*	-	Ai	Exc	-	-	-	-	-	-	SINGLET W
SR-Sc-mac	GAM	*Socarnes* sp.A	-	Ai	Exc	-	-	-	-	-	-	SINGLET W
SR-Sc-mac	GAM	*Onesimoides mediterraneus*	-	Ai	Exc	-	-	-	-	-	-	SINGLET W
SR-Sc-mac	GAM	*Podoprion bolivari*	-	Ai	Exc	-	-	-	-	-	-	SINGLET W
SS-Om-mic	ISO	*Eugerdella pugilator*	-	Ai	Exc	-	-	-	-	-	-	SINGLET W
SS-Pr-mei	GAM	*Westwoodilla rectirostris*	-	Ai	Exc	-	-	-	-	-	-	SINGLET W
EP-Om-mic	MYS	*Pseudomma cf. kruppi*	-	-	-	-	-	Exc	-	-	-	SINGLET C
EP-Pr-zoo	HYP	*Phronimella* sp.A	-	-	-	-	-	-	-	-	Exc	SINGLET E
EP-Pr-zoo	HYP	*Platyscelus* cf. *serratulus*	-	-	-	-	-	-	-	-	Exc	SINGLET E
EP-Pr-zoo	HYP	*Rhabdosoma brevicaudatum*	-	-	-	-	-	-	-	-	Exc	SINGLET E
EP-Om-mic	MYS	*Euchaetomera intermedia*	-	-	-	-	-	-	-	-	Exc	SINGLET E

TG: trophic groups; EP: water column/epibenthic, SR: surface, SS: subsurface; sed: sediment, mic: microfauna, mei: meiofauna, mac: macrofauna, zoo: zooplankton, Dt: detritus feeder, Su: suspension/filter feeder, Pr: predator, Sc: scavenger, Gr: grazer, Om: omnivorous; GAM: Gammaridea; HYP: Hyperiidea; SEN: Senticaudata; CUM: Cumacea; ISO: Isopoda; LOP: Lophogastrida; MYD: Mysida; TAN: Tanidacea; EUP: Euphausiacea; DEC: Decapoda; LEP: Leptostraca.

Table S2.1.2 List of species and trophic guilds and the code corresponding to the characterization of the species based on fidelity (Fidel) and constancy (Const) indices in the two study habitats. Do: dominant (top ten species); Ab: abundant (>1000 ind.); Co: constant; Ae: accessory; Ai: accidental; Exc: exclusive; Ele: elective; Pre: preferential; Aco: accompanying; Rar: accidental or rare; SINGLET: occurrence only in one station. **Codes: BASE** (constant); **BASE D** (constant and elective or exclusive); **AE D** (accessory and elective or exclusive); C: canyon; OS: open slope.

			Canyon				**Open slope**			**Code**
TG	**Order**	**Species**	Abund	Const	Fidel		Abund	Const	Fidel	
		Western slope								
EP-Om-mic	MYS	*Boreomysis arctica*	Do	Co	Aco	-	Do	Co	Pre	**BASE C-OS**
Ep-Om-mic	EUP	*Euphausia krohnii*	-	Co	Aco	-	-	Co	Pre	BASE C-OS
EP-Pr-zoo	GAM	*Rhachotropis caeca*	Do	Co	Pre	-	Do	Co	Aco	**BASE C-OS**
EP-Pr-zoo	GAM	*Bruzelia typica*	-	Co	Pre	-	-	Co	Aco	BASE C-OS
EP-Pr-zoo	GAM	*Rhachotropis rostrata*	-	Co	Pre	-	-	Co	Aco	BASE C-OS
EP-Pr-zoo	GAM	*Ileraustroe ilergetes*	-	Co	Aco	-	Do	Co	Pre	BASE C-OS
EP-Pr-zoo	GAM	*Rhachotropis glabra*	Do	Co	Pre	-	Do	Co	Aco	**BASE C-OS**
EP-Pr-zoo	EUP	*Nematoscelis megalops*	-	Co	Aco	-	Do	Co	Pre	BASE C-OS
EP-Pr-zoo	GAM	*Halice abyssi*	-	Co	Pre	-	-	Co	Aco	BASE C-OS
EP-Pr-zoo	GAM	*Syrrhoites* cf. *pusilla*	-	Co	Pre	-	-	Co	Aco	BASE C-OS
EP-Pr-zoo	GAM	*Eusirus longipes*	-	Co	Pre	-	-	Co	Aco	BASE C-OS
EP-Sp-fis	ISO	Gnathiidae und.	-	Co	Pre	-	-	Co	Aco	BASE C-OS
SR-Dt	GAM	*Mediterexis mimonectes*	-	Co	Aco	-	Do	Co	Pre	BASE C-OS
SR-Gr-mic	CUM	*Diastyloides serratus*	Do	Co	Pre	-	-	Co	Aco	BASE C-OS
SR-Gr-mic	GAM	*Leucon longirostris*	-	Co	Pre	-	-	Co	Aco	BASE C-OS
SR-Om-mic	ISO	*Munnopsurus atlanticus*	Do	Co	Pre	-	Do	Co	Aco	**BASE C-OS**
SR-Om-mic	ISO	*Belonectes parvus*	Do	Co	Aco	-	Do	Co	Pre	**BASE C-OS**
SR-Sc-mac	GAM	*Tryphosa nana*	-	Co	Pre	-	-	Co	Aco	BASE C-OS
SS-Pr-mei	GAM	*Bathymedon longirostris*	-	Co	Aco	-	Do	Co	Pre	BASE C-OS
SS-Pr-mei	GAM	*Bathymedon acutifrons*	Do	Co	Pre	-	-	Co	Aco	BASE C-OS
SS-Pr-mei	GAM	*Bathymedon banyulsensis*	-	Co	Aco	-	-	Co	Pre	BASE C-OS

			Canyon				Open slope			Code
TG	**Order**	**Species**	Abund	Const	Fidel		Abund	Const	Fidel	
SS-Pr-mei	CUM	*Campylaspis* sp.B	-	Co	Aco	-	-	Co	Pre	BASE C-OS
		Canyon								
EP-Om-mic	MYS	*Hemimysis abyssicola*	Do	Co	Exc	-	-	Ai	Rar	BASE D C
EP-Pr-zoo	GAM	*Rhachotropis grimaldii*	-	Co	Ele	-	-	Ae	Aco	BASE D C
EP-Pr-zoo	HYP	*Primno macropa*	-	Co	Ele	-	-	Ae	Aco	BASE D C
SR-Om-mac	ISO	*Natatolana cf borealis*	-	Co	Exc	-	-	Ai	Rar	BASE D C
SR-Om-mac	GAM	*Scopelocheirus hopei*	Do	Co	Ele	-	Do	Ae	Aco	**BASE D C**
SS-Pr-mei	GAM	*Synchelidium haplocheles*	Do	Co	Ele	-	-	Ae	Aco	BASE D C
Ep-Om-mic	MYS	*Parapseudomma calloplura*	-	Co	Pre	-	-	Ae	Aco	BASE C
EP-Pr-zoo	GAM	*Eusirus leptocarpus*	-	Co	Pre	-	-	Ae	Aco	BASE C
EP-Pr-zoo	HYP	*Hyperia* spp	-	Co	Pre	-	-	Ae	Aco	BASE C
SR-Gr-mic	CUM	*Eudorella* cf. *nana*	-	Co	Pre	-	-	Ae	Aco	BASE C
SR-Gr-mic	CUM	*Leucon macrorhinus*	-	Co	Pre	-	-	Ae	Aco	BASE C
SR-Om-mic	ISO	*Ilyarachna* cf. *longicornis*	-	Co	Pre	-	-	Ae	Aco	BASE C
SS-Pr-mei	GAM	*Monoculodes packardi*	-	Co	Pre	-	-	Ae	Aco	BASE C
EP-Om	DEC	*Eusergestes arcticus*	-	Ae	Ele	-	-	Ai	Aco	AE D C
EP-Om-mic	MYS	*Pseudomma affine*	-	Ae	Exc	-	-	-	-	AE D C
EP-Om-mic	MYS	*Mysidella biscayensis*	-	Ae	Exc	-	-	-	-	AE D C
Ep-Om-mic	MYS	*Erythrops neapolitanus*	-	Ae	Exc	-	-	Ai	Rar	AE D C
EP-Pr-mac	DEC	*Acanthephyra pelagica*	-	Ae	Ele	-	-	Ai	Aco	AE D C
EP-Pr-zoo	GAM	*Rhachotropis integricauda*	-	Ae	Exc	-	-	-	-	AE D C
EP-Pr-zoo	DEC	*Processa canaliculata*	-	Ae	Exc	-	-	-	-	AE D C
EP-Pr-zoo	GAM	*Nicippe tumida*	-	Ae	Exc	-	-	Ai	Rar	AE D C
EP-Pr-zoo	GAM	*Epimeria cornigera*	-	Ae	Ele	-	-	Ai	Rar	AE D C
EP-Pr-zoo	GAM	*Arculfia trago*	-	Ae	Ele	-	-	Ai	Rar	AE D C
EP-Pr-zoo	GAM	*Syrrhoe* cf. *affinis*	-	Ae	Ele	-	-	Ae	Aco	AE D C

			Canyon				**Open slope**			
TG	**Order**	**Species**	Abund	Const	Fidel		Abund	Const	Fidel	**Code**
EP-Su	CUM	Makrokylindrus josephinae	-	Ae	Exc	-	-	-	-	AE D C
SR-Gr-mic	CUM	*Leucon mediterraneus*	-	Ae	Exc	-	-	-	-	AE D C
SR-Gr-mic	CUM	*Leucon* sp.A	-	Ae	Exc	-	-	-	-	AE D C
SR-Gr-mic	CUM	*Eudorella* sp.A	-	Ae	Ele	-	-	Ai	Rar	AE D C
SR-Gr-mic	CUM	*Diastylis* cf. *jonesi*	-	Ae	Ele	-	-	Ae	Aco	AE D C
SR-Gr-mic	SEN	*Parvipalpus major*	-	Ae	Exc	-	-	-	-	AE D C
SR-Om-mic	DEC	*Richardina* sp.A	-	Ae	Exc	-	-	-	-	AE D C
SR-Om-mic	ISO	*Disconectes furcatus*	-	Ae	Ele	-	-	Ai	Rar	AE D C
SR-Pr-mac	DEC	*Aegaeon lacazei*	-	Ae	Ele	-	-	Ai	Rar	AE D C
SR-Pr-mei	GAM	*Metaphoxus simplex*	-	Ae	Ele	-	-	Ai	Aco	AE D C
SR-Sc-mac	GAM	*Lepidepecreum subclypeatum*	-	Ae	Ele	-	-	Ai	Aco	AE D C
SR-Sc-mac	LEP	Leptostraca sp.A	-	Ae	Ele	-	-	Ae	Aco	AE D C
SR-Su	GAM	*Ampelisca* cf. *diadema*	-	Ae	Exc	-	-	-	-	AE D C
SS-Om-mic	ISO	*Eugerda* cf. *tenuimana*	-	Ae	Ele	-	-	Ae	Aco	AE D C
SS-Om-mic	ISO	*Mirabilicoxa* sp.A	-	Ae	Ele	-	-	Ai	Aco	AE D C
SS-Pr-mei	CUM	*Nannastacus* sp.A	-	Ae	Exc	-	-	-	-	AE D C
SS-Pr-mei	CUM	*Cumella* sp.B	-	Ae	Ele	-	-	Ai	Rar	AE D C
SS-Pr-mei	GAM	*Westwoodilla caecula*	-	Ae	Ele	-	-	Ae	Aco	AE D C
SS-Pr-mei	GAM	*Bathymedon* cf. *monoculodiformis*	-	Ae	Ele	-	-	Ai	Aco	AE D C
SS-Pr-mei	CUM	*Campylaspis sulcata*	-	Ae	Ele	-	-	Ae	Aco	AE D C
SS-Pr-mei	GAM	*Deflexilodes griseus*	-	Ae	Ele	-	-	Ai	Aco	AE D C
U	GAM	*Amphilochus planieriensis*	-	Ae	Exc	-	-	-	-	AE D C
U	GAM	*Amphilochoides serratipes*	-	Ae	Ele	-	-	Ai	Rar	AE D C
U	GAM	*Carangoliopsis spinulosa*	-	Ae	Ele	-	-	Ae	Aco	AE D C
		Open slope								
EP-Su	CUM	*Makrokylindrus longipes*	-	Ae	Aco	-	-	Co	Ele	BASE D OS
SR-Gr-mic	CUM	*Vaunthompsonia caeca*	-	Ae	Aco	-	-	Co	Ele	BASE D OS

			Canyon				Open slope			
TG	**Order**	**Species**	Abund	Const	Fidel		Abund	Const	Fidel	**Code**
SS-Pr-mei	CUM	*Cyclaspis longicaudata*	-	Ae	Aco	-	-	Co	Ele	BASE D OS
EP-Om-mic	MYS	*Paramblyops rostratus*	-	Ae	Aco	-	-	Co	Pre	BASE OS
EP-Pr-zoo	HYP	*Vibilia armata*	-	Ae	Aco	-	-	Co	Pre	BASE OS
EP-Pr-zoo	LOP	*Eucopia unguiculata*	-	Ae	Aco	-	-	Co	Pre	BASE OS
EP-Pr-zoo	GAM	*Pseudotiron bouvieri*	-	Ae	Aco	-	-	Co	Pre	BASE OS
SS-Pr-mei	CUM	*Procampylaspis bonnieri*	-	Ae	Aco	-	-	Co	Pre	BASE OS
EP-Pr-zoo	GAM	*Halice walkeri*	-	Ai	Aco	-	-	Ae	Ele	AE D OS
EP-Su	CUM	*Makrokylindrus insignis*	-	-	-	-	-	Ae	Exc	AE D OS
SR-Dt	TAN	*Leviapseudes* cf. *segonzaci*	-	-	-	-	-	Ae	Exc	AE D OS
SR-Om-mic	ISO	*Disconectes phalangium*	-	Ai	Aco	-	-	Ae	Ele	AE D OS
SR-Om-mic	ISO	*Disconectes* sp.A	-	Ai	Rar	-	-	Ae	Ele	AE D OS
SR-Pr-mac	ISO	*Eurydice grimaldii*	-	-	-	-	-	Ae	Exc	AE D OS
SR-Pr-mac	GAM	*Stegocephaloides christianiensis*	-	Ae	Aco	-	-	Ae	Ele	AE D OS
SR-Sc-mac	GAM	*Tmetonyx similis*	-	-	-	-	-	Ae	Exc	AE D OS
SR-Sc-mac	GAM	cf. *Podoprion* sp.A	-	-	-	-	-	Ae	Exc	AE D OS
SR-Sc-mac	GAM	*Tryphosites longipes*	-	Ai	Aco	-	-	Ae	Ele	AE D OS
SR-Sc-mac	GAM	*Paracentromedon crenulatus*	-	Ai	Rar	-	-	Ae	Ele	AE D OS
SS-Pr-mei	CUM	*Campylaspis vitrea*	-	-	-	-	-	Ae	Exc	AE D OS
SS-Pr-mei	CUM	*Campylaspis horridoides*	-	Ae	Aco	-	-	Ae	Ele	AE D OS
U	ISO	Anthuridae sp.A	-	-	-	-	-	Ae	Exc	AE D OS
U	GAM	*Lepechinella manco*	-	Ae	Aco	-	-	Ae	Ele	AE D OS

TG: trophic groups; EP: water column/epibenthic, SR: surface, SS: subsurface; sed: sediment, mic: microfauna, mei: meiofauna, mac: macrofauna, zoo: zooplankton, Dt: detritus feeder, Su: suspension/filter feeder, Pr: predator, Sc: scavenger, Gr: grazer, Om: omnivorous; GAM: Gammaridea; HYP: Hyperiidea; SEN: Senticaudata; CUM: Cumacea; ISO: Isopoda; LOP: Lophogastrida; MYD: Mysida; TAN: Tanidacea; EUP: Euphausiacea; DEC: Decapoda; LEP: Leptostraca

2.2 Comparison of deep-sea crustacean suprabenthic community structure and biodiversity in the western and central Mediterranean Sea

Almeida, M., Plaiti, W, Tselepsides A., Sardà F., Cunha, M.R. (in preparation). Comparison of deep-sea crustacean suprabenthic community structure and biodiversity in the western and central Mediterranean Sea. To be submitted to Deep-Sea Research I.

Abstract

The deep-sea suprabenthic crustacean assemblages from the western and central Mediterranean Sea were studied from hauls collected at 600 m, 1000 m and 2000 m depths in the southern Balearic Sea and eastern Ionian Sea. Sedimentary variables were also sampled in the study locations. The taxonomic and trophic composition and biodiversity, abundance and community structure of the suprabenthic fauna were described. A total of 107 species were ascribed to eight sub-orders. Densities, number of species, number of trophic guilds and biodiversity were higher in the Balearic Sea than in the Ionian Sea and were associated to changes in trophic conditions in the sediments. Changes in the community composition and trophic structure also occurred at different longitudes. Maximum densities were found at 1000 m depth in both regions but while biodiversity was higher at the same depth in the Ionian Sea it increased with depth in the Balearic Sea. These results were related to the locally more favorable trophic conditions in each region. Overall, the oligotrophic gradient (i.e., quantity and quality of available food sources) that characterize the Mediterranean Sea, as well as spatial variability associated to local hydrodynamic features and topography in each region were the major drivers of biodiversity and community structure of suprabenthos in the Mediterranean slopes.

2.2.1 Introduction

The semi-enclosed Mediterranean Sea, one of the most oligotrophic deep-sea areas in the world, is characterized by a West-East productivity gradient generated by varying hydrographic features, productivity, and vertical fluxes of organic carbon to the seafloor (Estrada, 1996; Danovaro et al., 1999; Crispi et al., 2001; Millot and Taupier-Letage, 2005). The western Mediterranean is relatively more productive owing to the inflow of Atlantic water through the Gibraltar strait, river inputs and mesoscale variability in oceanographic processes (e.g. dynamics of Levantine Intermediate Water and Western Mediterranean Intermediate Water) (Estrada, 1996). The Central Mediterranean is known to be an oligotrophic area characterised by low concentration of suspended matter coupled with low particle fluxes (Napolitano et al., 2000; Boldrin et al., 2002). The eastern Mediterranean is extremely oligotrophic (Azov, 1986) because of the high nutrient depletion combined with high temperature (warm deep waters of 13-14°C) which leads to low productivity rates and reduced organic carbon flux to deeper waters (Psarra et al., 2000; Lampadariou et al., 2009). However, specific features in each of the Mediterranean regions, which differ both spatially and seasonally, may affect the downward particle fluxes to the seafloor and create locally relatively more productive areas (e.g. Tselepides and Lampadariou, 2004; Canals et al., 2013). The Gulf of Lion, influenced by river discharges and cascading events (Canals et al., 2006; Sanchez-Vidal et al., 2013) and the north Aegean Sea, influenced by the Black Sea inflow through the Dardanelles Strait, are examples of more productive areas in the western and eastern Mediterranean Sea, respectively (Poulos et al., 1997).

Food input to the seafloor is the main controlling factor of deep-sea standing stocks and biodiversity (Smith et al., 2008). In the oligotrophic Mediterranean Sea, the decrease in organic carbon fluxes with depth and longitude, is often associated to reduced faunal abundances (Tselepides et al., 2000; Danovaro et al., 2008; Tecchio et al., 2011b; Almeida et al., in press a). However, the effects of the oligotrophic gradient in the Mediterranean deep-sea biodiversity may be variable across deep-sea benthic components and across regions (Danovaro et al., 2010).

Suprabenthos, a less studied benthic compartment, is the faunal assemblage (mainly small crustaceans) living in the immediate vicinity of the seafloor which perform vertical migrations (Brunel et al., 1978). Suprabenthic organisms exploit organic and detritus particles and associated microbes, or prey on meiobenthos and plankton (Madurell et al., 2008; Fanelli et al., 2009) and are known to be an important food source for demersal fishes and decapods, including those with commercial value (Carrassón and Cartes, 2002). The trophic flexibility of the suprabenthic assemblages allows them to exploit oligotrophic environments with scarce or unpredictable food sources and therefore, suprabenthic organisms are a crucial link in the food webs of the Mediterranean continental slopes where fisheries are an important economic activity.

In the framework of the DESEAS project (an exploratory survey to collect data of the exploited and virgin stocks of the deep-sea shrimp *Aristeus antennatus*), several benthic compartments, (including mega-, macro- and meiofauna) were sampled in the Balearic and the Ionian Seas (Sardà et al., 2004). Community structure and distribution studies on fishes, crustacean megafauna and meiofauna were conducted and published (Company et al., 2004; D'Onghia et al., 2004; Sion et al., 2004; Tecchio et al., 2011a; Tselepides et al., 2004). The present study aims to describe the biodiversity and community structure of suprabenthos from these poorly investigated areas of the Mediterranean Sea, at depths between 600 and 2000 m. The results will be discussed in relation to the spatial variability of the environmental parameters and productivity levels.

2.2.2 Material and methods

2.2.2.1 Sample collection and processing

During the DESEAS trans-Mediterranean cruise carried out in 2001, on board the R/V García del Cid, two regions in the Mediterranean Sea were sampled: the southern Balearic Sea in the western basin (W) and the eastern Ionian Sea in the central basin (C), in June-July of 2001. Multiple corer samples (3 replicates) were collected in the study area at depths between 583 and 1735 m for the analyses of the sedimentary variables (see Tselepides et al., 2004 and Supplementary Material Table S2.2.1 for details).

Suprabenthic assemblages were collected in both basins at three depths (600, 1000 and 2000 m (Fig. 2.2.1) with a Macer-Giroq sledge that samples the motile fauna in the 10–50, 55–95 and 100-140 cm water layers above the seafloor (opening of the net: 40 cm height x 80 cm width; 500 µm mesh). This gear is equipped with a mechanical opening–closing system activated by the contact with the seafloor (see Cartes et al., 1994 for a detailed description of the gear). The sledge was towed at a speed of about 1–2 kn over the bottom during approximately 30 minutes. The metadata on the hauls are shown in Table 2.1.1. The samples were preserved in 10% buffered formalin aboard ship and in the laboratory they were washed and sieved through a 500 µm mesh and kept in 70% alcohol. The material was sorted into major groups.

The crustacean macrofauna, the focus of this study was identified to species level. However, the remaining groups such as demersal fishes, zooplankton (chaetognaths, gelatinosous taxa), meiofauna (copepods, ostracods and other non-crustacean taxa), and endobenthic components present in samples, were excluded from the analyses. The density of each taxon was calculated from the area (A, in m^2) swept by the sledge on the seafloor (haul length x net opening width) and expressed as number of individuals per 100 m^2 for the 10-140 cm water layer (total fauna). Densities were also expressed as individuals per 100 m^3 for the 10-50, 55-95 and 100-140 cm water layers (N1, N2 and N3, respectively).

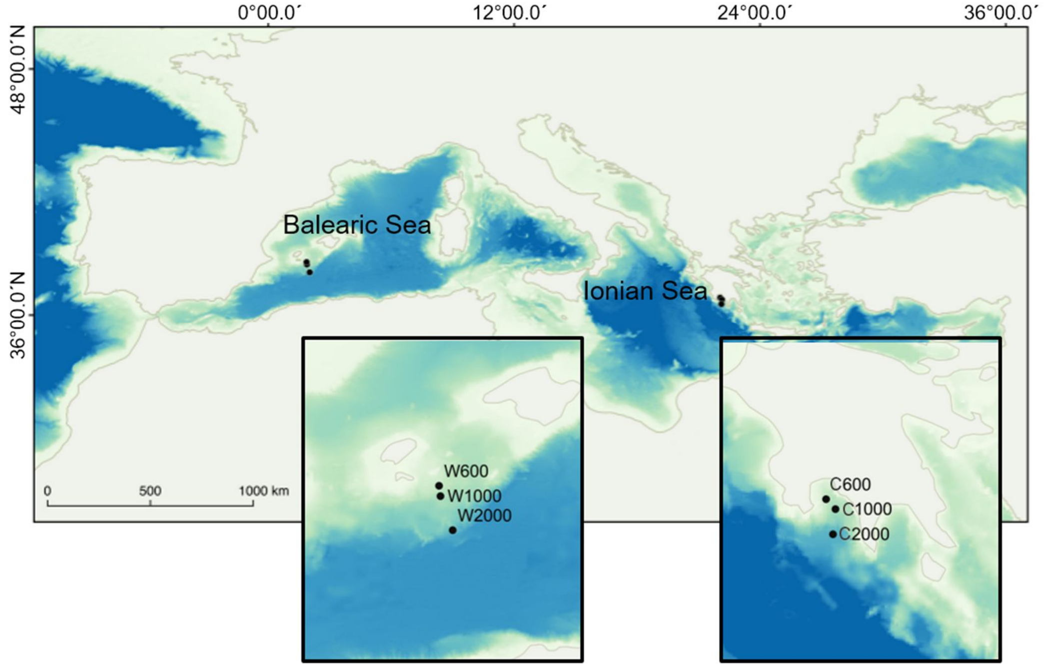

Figure 2.2.1 Location of sites sampled with a suprabenthic sledge in the bathyal Mediterranean Sea during DESEAS cruise in the two study areas. W (West basin, southern Balearic Sea) and C (Central basin, eastern Ionian Sea).

Table 2.2.1 Metadata of the samples taken from the two study areas in the bathyal Mediterranean Sea. West basin: southern Balearic Sea, Central basin: eastern Ionian Sea.

Sample code	Location	Date (d/m/y)	Hour^a (h:m)	Mean depth	Coordinates^a		Distance (m)	Area (m^2)
					Lat (N)	Lat (E)		
Haul1	Ionian (C)	28/06/2001	14:40	600	36°50'57"	22°04'02"	926	741
Haul2	Ionian (C)	28/06/2001	17:34	1100	36°45'46"	22°08'56"	1234.7	988
Haul3	Ionian (C)	28/06/2001	22.12	2150	36°32'37"	22°07'38"	1852	1482
Haull4	Balearic (W)	05/07/2001	12:47	2040	38°05'30"	02°02'43"	1852	1482
Haul5	Balearic (W)	05/07/2001	18:20	1000	38°28'26"	01°53'15"	1234.7	988
Haul6	Balearic (W)	05/07/2001	21:17	600	38°35'24"	01°52'18"	926	741

^{a}at the beginning of the haul

2.2.2.2 Data analysis

The number of species, Shannon–Wiener diversity (H'), Pielou (1969) evenness index (J') and Hurlbert (1971) expected number of species ES(n) were calculated for each sampling site. For multivariate analysis, the abundance data (density expressed as ind.100 m^{-3}) of the three nets, N1 (10-50 cm), N2 (55-95 cm) and N3 (100-140 cm) were kept separately in order to examine the vertical distribution of the suprabenthos. Furthermore, the samples were allocated to two geographical categories (W, C) and three bathymetric categories (600 m, 1000 m and 2000 m) used in the multivariate analyses to assess the effect of depth and longitude (W vs. C) on the biodiversity and structure of the assemblages. Non-metric multidimensional scaling (nMDS) was performed on the Bray–Curtis similarity matrix based on the abundance data, after square-root transformation. ANOSIM analysis (one-way ANOSIM) was used to assess for differences in the assemblages putatively related to the near-bottom vertical distribution, geographical location and depth. The indices and the multivariate analyses were performed using PRIMER v6 (Clarke and Gorley, 2006).

Suprabenthic trophic structure was estimated by allocating each taxon to a trophic guild defined by the food source/foraging behaviour, food type and size and feeding mode (adapted from Macdonald et al., 2010; with information compiled from Cartes, 1998a, Madurell et al., 2008, Fanelli et al., 2009). Food source was assigned to one of the following categories: water column or epibenthic (EP), seafloor surface (SR) and sediment subsurface (SS). Food type and size were described as sediment (sed), particulate organic matter (pom), microfauna (mic), meiofauna (mei), macrofauna (mac), phytodetritus (phy), zooplankton (zoo) and fish (fis). Feeding mode included deposit feeder (De), detritus feeder (Dt), suspension/filter feeder (Su), predator (Pr), scavenger (Sc), Suctorial parasite (Sp), grazer (Gr) and omnivorous (Om). Suprabenthic species were also ranked according to the six numerically dominant species per site.

2.2.3 Results

2.2.3.1 Environmental parameters

Data on surface sediment parameters measured in the study locations have been previously presented by Tselepides et al. (2004) (See Table S2.2.1, Supplementary material). In brief, sediments from both regions were similar in terms of grain size and consisted predominantly of silt and clay, except at 583 m in the Balearic Sea, characterized by silt-clay and fine sand. The concentration of total organic carbon was highest at intermediate depths (ca. 800 m) in both regions (0.6% in the Balearic Sea and 0.74% in the eastern Ionian Sea) and TON (total organic nitrogen) varied between 0.07 and 0.09%. At all depths, C/N (carbon to nitrogen ratio) was higher in the eastern Ionian

Sea (10.5 at 600 m; 11.0 at 800 m; 8.5 at 1735 m) than in the Balearic Sea (6.0 at 583 m; 7.9 at 814 m; 8.2 at 1429 m). Chlorophyll a values ranged from 0.12 to 0.67 $\mu g.g^{-1}$, with the highest values found in the Balearic Sea. The concentration of phaeopigments and CPE (chloroplastic pigment equivalent) were in general higher in the Balearic Sea at all depths with maxima at 600 m depth in the Balearic Sea (1.18 and 1.29 $\mu g.g^{-1}$ respectively), and at 800 m depth in the eastern Ionian Sea (1.46 and 1.19 $\mu g.g^{-1}$ respectively). These values suggest a higher input of organic matter, expressed by the higher values either of chlorophyll a, phaeopigments or CPE, in the Balearic Sea.

2.2.3.2 Suprabenthic assemblage composition and abundance

A total of 4664 specimens collected from the six hauls were ascribed to 107 species of eight sub-orders (Amphipoda, Cumacea, Isopoda, Lophogastrida, Mysida, Tanaidacea, Decapoda, Euphausiacea). However, it should be noted that from the material collected in the hauls 2 and 4, the sub-order Isopoda was not identified to species level (owing to the loss of samples after sorting and major group abundance counts). In general, a higher number of species, trophic guilds and individuals (more than 90.0% of the total fauna) was found in the near-bottom water layer (10-50 cm above the bottom) (Table 2.2.2). This trend was observed for amphipods, cumaceans, isopods and mysids whereas decapods and euphausiids were well represented in all water layers.

Isopods (32.7% of total abundance, 13 species), amphipods (27.2% of total abundance, 41 species) and mysids (21.9%, 10 species) were the most abundant groups followed by cumaceans (13.0%, 19 species), decapods (2.4%, 14 species) and euphausiids (2.6%, 7 species) and were represented in all samples (Fig. 2.2.2). The other groups (lophogastrids and tanaids; <1%, 3 species) were only represented in two hauls and by few individuals. Although in two hauls (trawl 2 and 4) the identification of the sub-order Isopoda to species level was not possible to achieve, the general trend indicates that amphipods were the most species-rich group.

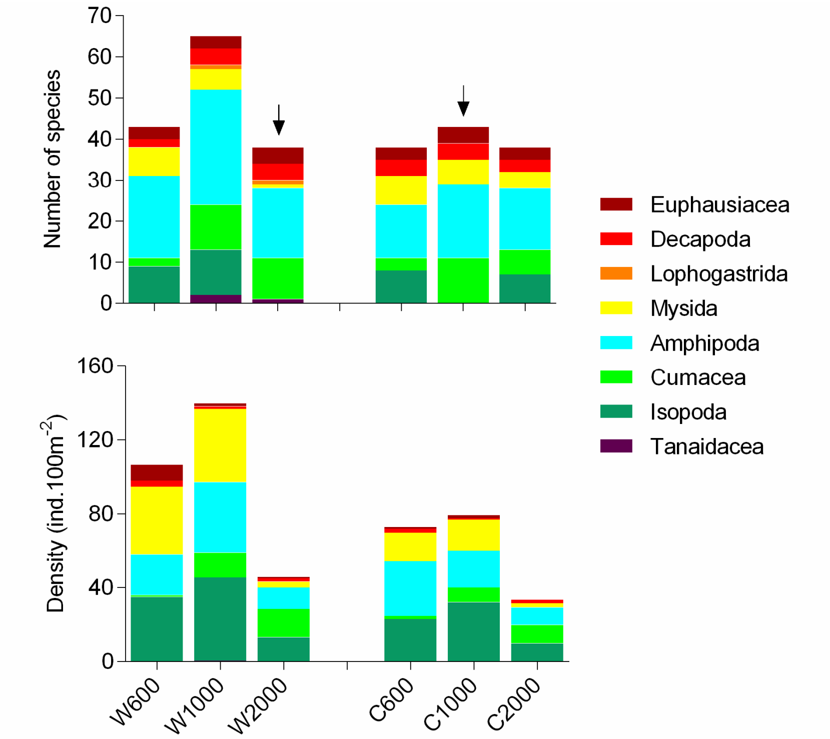

Figure 2.2.2 Number of species and density (ind.100 m^{-2}) of the major taxonomic groups of suprabenthos from the bathyal Mediterranean Sea. W: southern Balearic Sea; C eastern Ionian Sea. .↓: Isopoda species are not included.

The total number of species was higher at intermediate depths and the lowest number of trophic guilds was found at shallowest sites; comparing both basins, the highest number of species and trophic guilds was found in the Balearic Sea (Fig. 2.2.2, Table 2.2.2). The amphipods, cumaceans and isopods attained the highest number of species at intermediate depths (amphipods: from 13 species at W600 to 28 species at W1000; cumaceans: from 2 species at W600 to 11 species at W1000; isopods: from 7 species at E2000 to 11 species at W1000). The mysids attained the highest number of species at the shallowest sites (7 species at W600 and E600 in contrast to only one species at E2000). The other groups presented fewer fluctuations between sites (Fig. 2.2.2, Table 2.2.2).

The variation in suprabenthic densities among sites is shown in Fig. 2.2.2 and Table 2.2.2. The highest density of suprabenthos was recorded at intermediate depths (1000 m), followed by a sharp decrease at 2000 m. In the Balearic Sea, suprabenthic density ranged from 45.6 to 106.5 ind.100 m^{-2}, showing a clear peak at 1000 m, mainly due to the increase of amphipods, cumaceans and isopods. In the Ionian Sea, suprabenthic density ranged from 33.6 to 79.3 ind.100 m^{-2} but with less marked differences between 600 m and 1000 m depth. Overall higher densities were observed in the Balearic Sea.

The isopods and amphipods dominated the assemblages and were abundant at all sites (Fig. 2.2.3). The relative contribution of isopods to abundance varied between 28.1% at W2000 to 40.4% at E1000; the amphipods varied between 20.9% at W600 to 40.6% at E600. The mysids were well represented at the shallowest sites; their relative contribution to abundance varied between 6.6% at E2000 to 34.4% at W600. Contrastingly, the cumaceans were well represented at the deepest sites; their relative contribution to abundance varied between 0.9% at W600 to 33.7% at W2000 (Fig. 2.2.3).

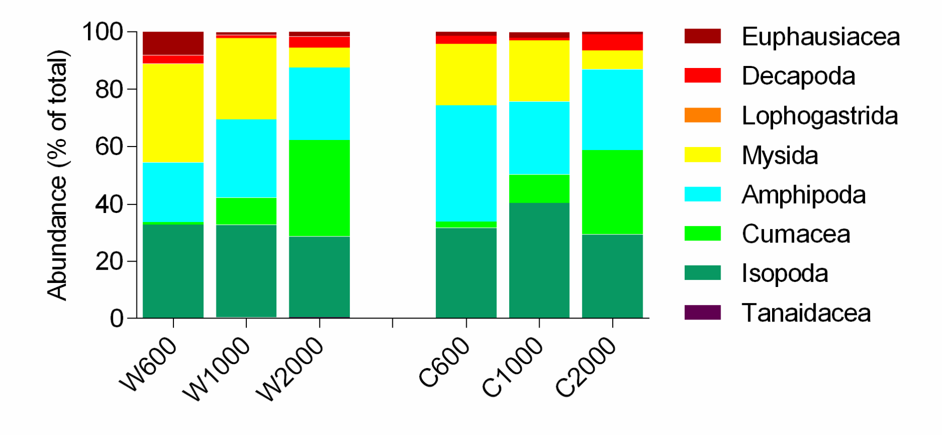

Figure 2.2.3 Relative abundance (%) of the major taxonomic groups of suprabenthos from the bathyal Mediterranean Sea. W: southern Balearic Sea; C: eastern Ionian Sea.

Table 2.2.2 Abundance and biodiversity (taxonomic and trophic) of suprabenthos illustrating the near-bottom vertical distribution and the total assemblage in the sites sampled. W: southern Balearic Sea; C: eastern Ionian Sea; N1:10-50 cm, N2: 55-95 cm and N3:100-140 cm water layers; A: abundance; S: number of species; H': Shannon-Wiener diversity index (ln-based); ES$_{(100)}$/ETG$_{(100)}$: Hulbert's expected number of species/trophic groups diversity index, J': Pielou evenness index. Note: The sub-order Isopoda was considered to be represented by one taxon and one trophic guild.

Site	Water layer	A	Density		Taxonomic				Trophic			
			ind.100 m^{-3}	ind.100 m^{-2}	S	H'	J'	ES$_{(100)}$	TG	H'	J'	ETG$_{(100)}$
W600	N1	676	228.1		33	1.96	0.56	16	9	1.26	0.575	5.6
	N2	74	25		16	1.88	0.679	16	3	0.78	0.707	3
	N3	39	13.2		12	2.16	0.868	12	5	1	0.624	5
	Total	789		106.5	35	2.11	0.593	17.2	10	1.27	0.551	5.6
W1000	N1	1315	332.8		54	2.54	0.637	22.2	11	1.64	0.683	7.7
	N2	47	11.9		16	2.48	0.893	16	6	1.58	0.88	6
	N3	17	4.3		10	2.12	0.92	10	4	1.01	0.725	4
	Total	1379		139.6	55	2.61	0.651	23.5	11	1.65	0.688	7.9
W2000	N1	637	107.5		35	2.64	0.742	21.9	12	1.69	0.679	7.6
	N2	22	3.7		10	2.14	0.928	10	5	1.33	0.825	5
	N3	17	2.9		6	1.7	0.951	6	3	1.01	0.921	3
	Total	676		45.6	39	2.76	0.754	24.2	12	1.74	0.7	8.2
C600	N1	515	173.8		27	1.85	0.562	14.3	7	1.26	0.649	5
	N2	13	4.4		8	1.98	0.952	8	5	1.42	0.885	5
	N3	11	3.7		8	2.03	0.974	8	4	1.17	0.843	4
	Total	539		72.8	31	1.94	0.566	15.8	7	1.27	0.654	5.2
C1000	N1	743	188.1		40	2.16	0.585	18.7	10	1.6	0.694	8.2
	N2	18	4.6		10	2.21	0.958	10	7	1.63	0.837	7
	N3	22	5.6		9	1.96	0.89	9	6	1.33	0.744	6
	Total	783		79.3	44	2.26	0.597	20.1	11	1.62	0.676	8.4
C2000	N1	433	73.1		28	2.06	0.62	15.6	10	1.54	0.669	7.5
	N2	58	9.8		16	2.24	0.807	16	10	1.54	0.669	7.5
	N3	7	1.2		4	1. 15	0.832	4	7	1.4	0.717	7
	Total	498		33.6	32	2.18	0.629	16.4	10	1.57	0.683	7.5
600					49			18.4	10			5.5
1000					73			23.7	11			8.2
2000					52			24	13			8.3
W					77			26.5	13			7.8
C					63			22.4	12			8.6
All					95			26.3	13			8.2

The taxonomic and trophic structure of the assemblages changed with depth and longitude (Figs. 2.2.3-2.2.4): a decrease in the relative abundance of epibenthic omnivore mysids, with depth and with longitude was observed concomitant with the increase in the relative abundance of cumaceans, mostly surface grazers on microbiota. Subsurface predators on meiofauna were only well represented in the Balearic Sea and their relative contribution to total abundance increased with depth. On the other hand, epibenthic predators on zooplankton (e.g. eusirid amphipods) and macrofauna (e.g. decapods) showed higher contributions in the Ionian basin (especially at 600 m). The relative contribution of isopods (mostly surface omnivores) remained relatively constant at all depths and in both basins.

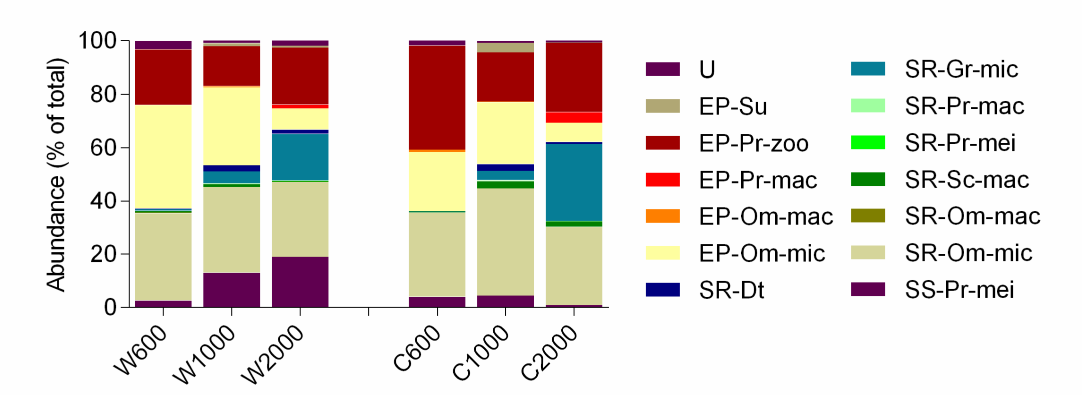

Figure 2.2.4 Relative abundance (%) of the trophic groups of suprabenthos from the bathyal Mediterranean Sea. W: southern Balearic Sea; C: eastern Ionian Sea. EP: water column/ epibenthic; SR: surface; SS: subsurface; mic: microfauna; mei: meiofauna; mac: macrofauna; zoo: zooplankton; fis: fish; Dt: detritus feeder; Su: suspension/filter feeder; Pr: predator; Sc: scavenger; Sp: sectorial parasite; Gr: grazer; Om: omnivorous; U: unknown. Note: The order Isopoda was allocated to the trophic guild SR-Om-mic.

Table 2.2.3 shows the percent contribution of the six dominant species in each site. The amphipod *Rhachotropis caeca* (7.3-30.6%) and the isopod *Munnopsurus atlanticus* (22.1-24.8%) were always ranked amongst the 6 dominant species. Note that the first dominant taxa in sites W2000 and C1000 is also probably *M. atlanticus* although isopod species in these samples could not be determined. The mysid *Boreomysis artica* (4.8-23.1%) was also ranked amongst the 6 dominant species in most of the sites, except for E600. The mysids *Calyptomma puritani* (9.2-15.4%) at 1000 m depth in the Balearic Sea and at 600 m in the Ionian Sea and *Parerytrhops lobiancoli* (2.9-3.4%) at 1000 m depth in both basins were also among the dominant species. The cumaceans occupy the leading ranks at the deepest sites: *Procampylaspis armata* (9.6%) and *Vaunthompsonia* sp. (6.1%) in the Balearic Sea, *Diastyloides serrata* in the Ionian Sea (6.0%) and *Platysympus typicus* (5.5-21.5%) in both basins.

Table 2.2.3 Six dominant species of suprabenthos collected in each sampling site. W: southern Balearic Sea; C: eastern Ionian Sea. EP: epibenthic; SR: surface; SS: subsurface; mic: microfauna; mei: meiofauna; mac: macrofauna; zoo: zooplankton; fis: fish; Dt: detritus feeder; Su: suspension/filter feeder; Pr: predator; Sc: scavenger; Sp: sectorial parasite; Gr: grazer; Om: omnivorous; U: unknown. Note: The order Isopoda was allocated to the trophic guild SR-Om-mic.

Balearic Sea				**Ionian Sea**			
W600			%	**C600**			%
ISO	SR-Om-mic	*Munnopsurus atlanticus*	23.2	AMP	EP-Pr-zoo	*Rhachotropis caeca*	30.6
MYS	Ep-Om-mic	*Boreomysis arctica*	23.1	ISO	SR-Om-mic	*Munnopsurus atlanticus*	23.2
AMP	EP-Pr-zoo	*Rhachotropis caeca*	11.9	MYS	Ep-Om-mic	*Calyptomma puritani*	15.4
ISO	SR-Om-mic	*Belonectes parvus*	4.1	AMP	EP-Pr-zoo	*Rhachotropis rostrata*	2.8
EUP	EP-Pr-zoo	*Nematoscelis megalops*	3.7	MYS	Ep-Om-mic	*Parapseudomma calloplura*	2.0
MYS	Ep-Om-mic	Mysida und	3.5	AMP	SS-Pr-mei	*Bathymedon longirostris*	1.9
			69.5				75.9
W1000				**C1000**			
ISO	SR-Om-mic	*Munnopsurus atlanticus*	24.8	ISO	SR-Om-mic	Isopoda	38.1
MYS	Ep-Om-mic	*Boreomysis arctica*	13.9	AMP	EP-Pr-zoo	*Rhachotropis caeca*	14.3
MYS	Ep-Om-mic	*Calyptomma puritani*	9.2	MYS	Ep-Om-mic	*Boreomysis arctica*	13.2
AMP	EP-Pr-zoo	*Rhachotropis caeca*	8.4	CUM	EP-Su	*Makrokylindrus longipes*	3.4
AMP	SS-Pr-mei	*Bathymedon longirostris*	4.6	MYS	Ep-Om-mic	*Parerythrops lobiancoli*	3.4
MYS	Ep-Om-mic	*Parerythrops lobiancoli*	2.9	AMP	SR-Dt	*Mediterexis mimonectes*	2.6
			63.8				75.0
W2000				**C2000**			
ISO	SR-Om-mic	Isopoda	28.1	ISO	SR-Om-mic	*Munnopsurus atlanticus*	22.1
CUM	SS-Pr-mei	*Procampylaspis armata*	9.6	CUM	SR-Gr-mic	*Platysympus typicus*	21.5
AMP	EP-Pr-zoo	*Rhachotropis caeca*	7.3	AMP	EP-Pr-zoo	*Rhachotropis caeca*	17.5
CUM	SR-Gr-mic	*Vaunthompsonia caeca*	6.1	CUM	SR-Gr-mic	*Diastyloides serrata*	6
MYS	Ep-Om-mic	*Boreomysis arctica*	5.6	MYS	Ep-Om-mic	*Boreomysis arctica*	4.8
CUM	SR-Gr-mic	*Platysympus typicus*	5.5	DEC	EP-Pr-mac	*Acanthephyra eximia*	3.8
			62.2				75.7

2.2.3.3 Biodiversity indices

Figure 2.2.5 shows the taxonomic and trophic biodiversity for each sampling site. Taxonomic diversity indices (H', ES) illustrate clear differences between basins, with the highest diversity found in the Balearic Sea (ES_{100}: 26.5) and the lowest in the Ionian Sea (ES_{100}: 22.4). Patterns of suprabenthic diversity related to depth differed between the investigated regions. In the Balearic Sea, the lowest diversity was found at the shallowest site (600 m: H': 2.11, ES_{100}: 17.2) and the deeper sites presented similar values (1000 m: H': 2.61, ES_{100}: 23.5; 2000 m: H': 2.76, ES_{100}: 24.2). In contrast, in the Ionian Sea, as for the number of species, diversity was higher at 1000 m depth (H': 2.26, ES_{100}: 20.1) with lower values at the other sampled depths (H': 1.94-2.18 and ES_{100}: 15.8-16.4). Overall, differences between the two regions were accentuated at greater depths with considerably lower values of the taxonomic diversity indices in C2000.

Trophic diversity differed between the depths investigated but no trends emerge when the regions are compared. The lowest trophic diversity was found at the shallowest site (ES_{100}: 5.5) and the others depths show considerably higher values (ES_{100}: 8.2-8.3). In fact, taxonomic and trophic trends in the Ionian Sea are similar but in the Balearic Sea the highest taxonomic diversity at the deepest site is not mirrored by a similar increase in the trophic diversity.

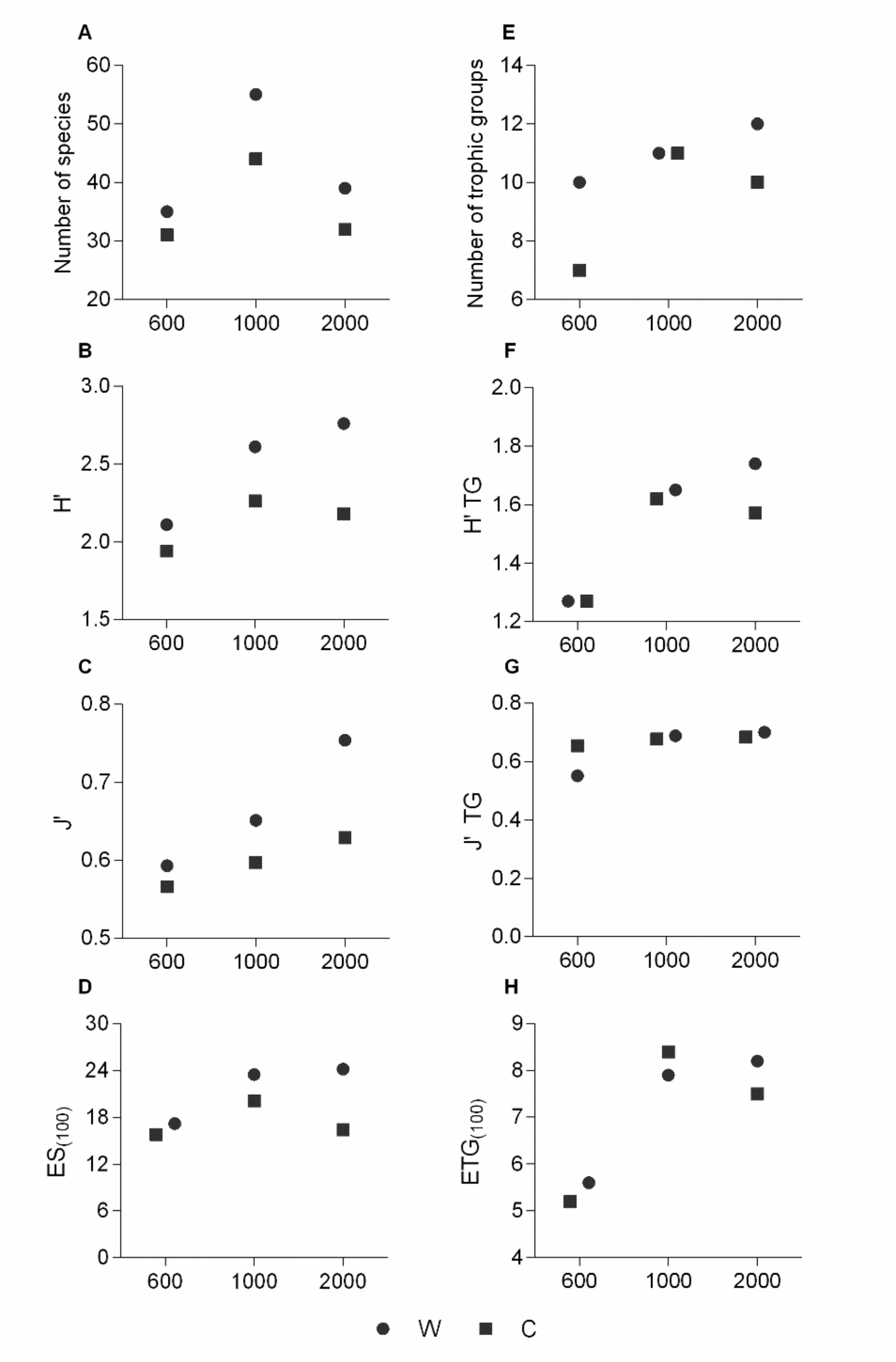

Figure 2.2.5 Biodiversity (taxonomic –A, B, C; trophic –D, E, F of the suprabenthic assemblages from the bathyal Mediterranean Sea. H': Shannon-Wiener diversity index (H', ln-based); J: Pielou evenness index (J'); $ES_{(100)}$: Hurlbert's expected number of species; TG: trophic groups; W: southern Balearic Sea; C: eastern Ionian Sea.

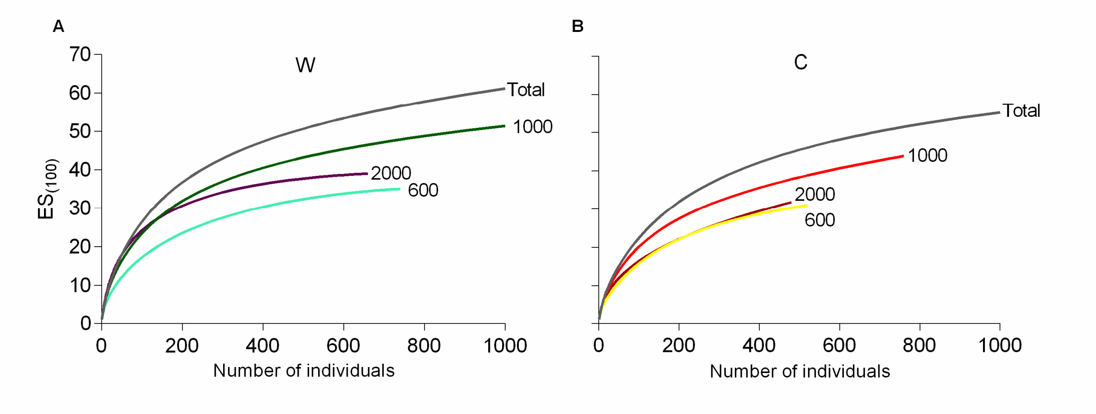

Figure 2.2.6 Rarefaction curves (Hurlbert's expected number of species) of the suprabenthic assemblages from the bathyal Mediterranean Sea. Comparison of the southern Balearic Sea (W) and eastern Ionian Sea (C) at 600, 1200 and 2000 m.

2.2.3.4 Multivariate analysis

The MDS plot (note: the sub-order Isopoda was considered in this analysis as a single taxon) illustrates the great heterogeneity in the composition of suprabenthos of the six sites (Fig. 2.2.7). In terms of the near-bottom vertical distribution of suprabenthos the MDS shows differing patterns: a clear segregation of the samples from the near-bottom water layer (N1) is observed while a larger dispersion in the plot of the samples from the upper layers (N2, N3) may result from the impoverished assemblages in terms of number of species and density observed in these layers by one order of magnitude. The ANOSIM shows that differences in the community structure are statistically significant in terms of the near-bottom vertical distribution (Table 2.2.4). The MDS (Fig. 2.2.7) also shows that the samples representing assemblages from different regions occupy well-defined positions in the plot while the separation by bathymetric level is not clear. This is confirmed by the ANOSIM tests that show significant differences between regions, but not among bathymetric levels (Table 2.2.4). These differences are mostly related to density fluctuations of the most abundant species.

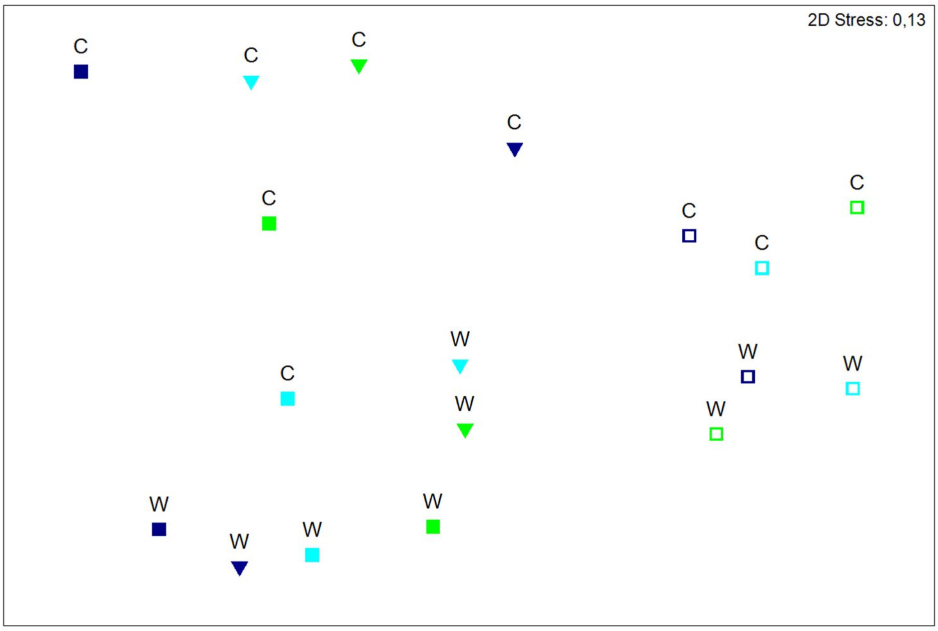

Figure 2.2.7 MDS (multidimensional scaling) 2D ordination plot based on abundance data (expressed as ind.100 m^{-3}) of the suprabenthic assemblages collected in the bathyal Mediterranean Sea. W: southern Balearic Sea; C: eastern Ionian Sea. Different symbols indicate different water layers (open symbols: 0 to 50 cm water layer; full inverted triangles: 50-95 cm water layer; full squares: 100-140 cm water layer). Different colours indicate different depths (green: 600 m; light blue: 1000 m; dark blue: 2000 m).

Table 2.2.4 Results of the one way ANOSIM global and pairwise tests. ANOSIM test 1 factor “net” (near-bottom vertical distribution, N1: 10–50 cm (near-bottom) water layer, N2: 55–95 cm water layer, N3: 100–140 cm water layer); ANOSIM test 2: factor “area” (geographic location, W: southern Balearic Sea; E: eastern Ionian Sea); ANOSIM test 3: factor “depth” (600, 1000 and 2000 m water depth). P: significance level in percentage.

	Sample Statistic	Permutation used	Significant statistics	P
Anosim test 1: net				
Global value	0.562	999	0	0.1**
Pairwise tests				
N1, N2	0.7	462	0	0.2**
N1, N3	0.87	462	0	0.2**
N2, N3	-0.041	462	116	58.7 ns
Anosim test 2: area (W vs. C)				
Global value	0.254	999	16	1.7*
Anosim test 3: depth				
Global value	0.052	999	40	25.3 ns

* significant; **very significant; ns: not significant.

2.2.4 Discussion

Studies on suprabenthic assemblages in the bathyal Mediterranean are concentrated in the western basin and mostly on the upper slopes (e.g. Cartes, 1998b; Cartes and Sorbe, 1996, 1999; Cartes et al., 2003, 2011) while few studies were performed in the eastern basin (Sorbe and Galil, 2002; Madurell and Cartes, 2003; Galil, 2004; Koulouri et al., 2013) and one similar Trans-Mediterranean study was conducted at greater depths (1000, 2000 and 3000 m) including the South Balearic Sea, West Ionian Sea and South of Crete (Almeida et al., in press a).

In this study a decrease in suprabenthic densities and number of species was observed from the near-bottom to the upper layers which is reflected by the high dispersion of the latter samples in the MDS plot. This is a general trend found in other suprabenthic assemblages where most of the fauna is found in the vicinity of the seafloor (e.g. Cartes et al., 2003; Frutos and Sorbe 2014; Almeida et al., in press a). Most of the peracarids and eucarids reported in previous suprabenthic studies on the bathyal assemblages from the Mediterranean Sea were also found in the present study (Cartes and Sorbe 1995, 1997, 1999; Cartes et al., 2003; Madurell and Cartes, 2003). Suprabenthos was composed by mysids, amphipods, isopods and cumaceans with a wide spectrum of feeding guilds. The dominance of omnivores with mixed diets (e.g. mysids and asellote isopods feeding alternately on detritus and small invertebrates) and predators with relatively high motility (e.g. eusirid amphipods) confirms the oligotrophic characteristics of the area, as these feeding strategies are found in environments that generally have low availability of food, such as in the deep Mediterranean Sea (Tselepides et al., 2000; Fanelli et al., 2009; Baldrighi et al., 2014). However, their respective contribution to total abundance may vary according to geographical site and sampling season (Almeida et al., in press b). Our results show that isopods were the most abundant group in contrast to other studies in the Mediterranean Sea which reported a general numerical dominance of amphipods and mysids (Cartes et al., 2008; Almeida et al., in press a,b). However, Cartes (1998b) showed the dominance of isopods in the more productive upper slopes of the Catalan Sea in particular seasons: in the winter in submarine canyons and in the spring in the open slopes. This trend was also observed in the northeast Atlantic suprabenthic assemblages, where at bathyal depths, the most abundant group were asellote isopods (Elizalde et al., 1993; Sorbe and Elizalde, 2013; Sorbe, 1999). The high abundance of isopods, and particularly the dominance of *Munnopsurus atlanticus* (predators on foraminifera and feeding on detritus) at all sites may represent a seasonal peak in the population dynamics of this species. Previous studies in the bathyal western Mediterranean and in the Bay of Biscay suggested a coupling between a peak in abundances of *M. atlanticus* recorded in June-July and the increase in foraminiferal densities, in response to the increase in primary production and organic matter supply to the benthos (Cartes et al., 2000; Sorbe and Elizalde, 2014) or to temporal variability in the inputs of organic matter derived from river discharges (e.g. high inputs observed in the winter in the Catalan slopes; Cartes, 1998b).

Several studies in the Mediterranean open slopes reported low abundances and number of species when compared to the Atlantic region (Emig, 2004). The observed values of density, diversity and number of species are in the range of the values reported from other suprabenthic assemblages from Mediterranean open slopes, however these are lower than those found in other deep-sea regions at similar depths (Table 2.2.5). This general trend is mainly related to the prevailing oligotrophic conditions in the Mediterranean Sea and is clearly evident when the western and eastern basins are compared (Danovaro et al., 1999).

Balearic Sea vs. Ionian Sea

Several studies in the Mediterranean open slopes reported a decline in the abundance, biomass and number of species of the benthic fauna (i.e. meiofauna, macrofauna, megafauna) with increasing depth and from the northwestern to southeastern areas (Tselepides et al., 2000, 2004; Tecchio et al., 2011a; Baldrighi et al., 2014; Almeida et al., in press a).

The West-East gradient of decreasing surface productivity is associated to a decrease in the quantity and quality of detritus reaching the seafloor (Danovaro et al., 1999; Psarra et al., 2000) which may considerably reduce the availability of food for the benthos. From primary production estimates it has been calculated that the carbon export from the euphotic layer to 1000 m depth is equivalent to about 10% in the Gulf of Lions (northwestern Mediterranean) and 2-3% in the Cretan Sea (eastern Mediterranean) and chlorophyll a concentrations in the sediment, at similar depths, are 2–3 times higher in the western basin (Danovaro et al., 1999). This is in agreement with the higher values of chlorophyll a, phaeopigments and CPE, measured in the Balearic Sea sediments in comparison to the ones from the eastern Ionian Sea (Tselepides et al., 2004). Moreover, C/N values around 8 or lower as the ones found in the Balearic Sea, are indicative of higher quality and predominantly marine origin of the organic matter (Cunha et al., 2011). This may explain the generally impoverished assemblage, both in terms of densities and number of species reported here for the Ionian Sea. The lower relative contributions of surface and subsurface predators feeding on meiofauna (e.g. several oedicerotid amphipods and nannastacid cumaceans) and a higher relative contribution of predators on zooplankton (e.g. eusirid amphipods) in the Central basin may reflect a lower availability of food sources in the sediments at this region when compared to the West basin. These trends were also documented by Almeida et al. (in press a), who reported higher abundances in the Balearic Sea in comparison with the West Ionian Sea and South of Crete and changes in the taxonomic and trophic structure along the West-East gradient as a result of increasing oligotrophic conditions.

Bathymetric trends

The decrease in abundances with depth for several benthic compartments is related to the decrease in surface productivity and distance to coastal areas (Rex and Etter, 2010 and references therein). There are, however, exceptions to this trend, which have been mostly attributed to the occurrence of localized areas of organic enrichment (e.g. submarine canyons, trenches) where higher standing stocks are found in comparison to the surrounding areas (Cartes, 1998b, Vetter and Dayton, 1998; Tselepides and Lampadariou, 2004). We found higher densities at intermediate depths in both regions, although more pronounced in the Balearic Sea. This is in agreement with observations from suprabenthic assemblages reaching maximum densities at ca. 1000 m depth in the South Balearic Sea, West Ionian Sea and South of Crete (Almeida et al., in press a) and other benthic compartments (meio- and megabenthos) sampled in the same sampling period reported by Company et al. (2004), Tselepides et al. (2004) and Tecchio et al. (2011a).

In the eastern Ionian Sea higher biodiversity was observed at this bathymetric level. Higher values of TOC, chlorophyll a, phaeopigments and CPE measured in the sediments at 800 m are indicative of high food availability and quality. In the Balearic Sea the most diverse (H', ES) and even (J') assemblages were found at 1000 and 2000 m depth. High productivity at surface waters, coastal input coupled with downslope shelf-water cascading events (Danovaro et al., 1999; Canals et al., 2006), may supply this basin with higher, more diversified and fresh organic matter to the sediments which may sustain a diverse assemblage at deeper sites.

The analysis of trophic diversity revealed clear differences among depths but no evident differences between basins. The lowest trophic diversity was observed at the shallowest sites, probably related to an opportunistic response (high dominance) of a few feeding guilds, namely highly mobile groups feeding on the water column (e.g. mysids) or zooplankton predators in response to putative higher food sources available in the water column rather than in the sediment. In fact, the migratory behavior of mysids may be limited with increasing depth (Cartes and Sorbe, 1995; Cartes et al., 2011) which could explain the decrease in the relative abundance of this group and the relative increase of other suprabenthic groups. With increasing depth, several cumacean species relaying on food sources from the sediment gained importance probably in response to the increase of TOC in the sediments (Tselepsides et al., 2004).

2.2.5 Conclusions

The suprabenthic abundance and biodiversity support previous observations reporting a longitudinal decreasing trend from the West to the East Mediterranean associated to different trophic conditions. The suprabenthic community and trophic structure also changed with longitude. Bathymetric trends differed between regions and were associated to spatial variation of vertical and lateral fluxes of organic matter to the seafloor. In the East Ionian Sea, located in a relative more productive region in the Central Mediterranean due to the influence of the Black Sea inflow, suprabenthic assemblages are likely to depend primarily on the organic matter fluxes of pelagic origin whereas in the Balearic Sea, located near the Strait of Gilbraltar and influenced by DSWC and inputs form submarine canyons, additional sources of organic carbon may be drivers of suprabenthic biodiversity. The suprabenthic assemblages appear to be influenced by temporal variability in organic matter inputs as showed by the numerical dominance of the isopod *Munnopsurus atlanticus.*

Table 2.2.5. Overview of literature published in the past three decades on suprabenthic community structure and biodiversity at depths greater than 200 m. S: number of species; H’: Shannon-Wiener diversity index.

Region	Depth range (m)	Density (ind.100m^{-2})	S	H'	Reference
NE Atlantic					
Meriadzek Terrace	200-1250	~100-14000	17-102	1.93-3.84	Vanquickelberghe (2005)
(Bay of Biscay)	200-700	226-1300	67-108	-	Dewicke (2002)
Cap-Ferret area (Bay of Biscay)	425-1043	271.8-1383.1	63-116	2.78-5.53	Elizalde et al. (1993)
	346-3070	189-1588	-	-	Dauvin et al. (1995)
	2400,3000	283.3-525.3	-	-	Sorbe (1999)
	386–420	82-3199	31-76	2.30-4.01	Sorbe and Elizalde (2014)
Capbreton area (Bay of Biscay)	1000	-	63	3.04-5.03	Marquiegui and Sorbe (1999)
	391-405	391	56	-	Sorbe et al. (2010)
	175-1000	752-2640	48-102	3.83-5.72	Frutos and Sorbe (2014)
Portuguese continental margin	21-299	916.1	74	4.15	Cunha et al. (1997)
Mediterranean Sea					
Catalan Sea	389-1355	24.4-2150.1	-	-	Cartes (1998b)
	189-1645	24.7-190.2	-	-	Cartes et al. (2002)
	524-670	530.6-538.8	-	-	Cartes et al. (2009)
	466-1517	8.5-515.6	21-73	1.75-3.01	Almeida et al. (in press b)
Balearic Islands	150-750	10.0-277.7			Cartes et al. (2008)
	150-750		8-57.8	1.55-3.23	Cartes et al. (2011)
Balearic Islands and Catalan Sea	249-1622	-	34-144	1.27-5.16	Cartes et al. (2003)
South Aegean Sea	50-300	12-248	8-42	-	Koulouri et al. (2013)
Balearic Sea, Ionian Sea and south of Crete	1200, 2000, 3000	3.5-36.5	23-53	2.11-2.92	Almeida et al. (in press a)
Balearic Sea and Ionian Sea	600, 1000, 2000	33.6-139.6	31-55	1.94-2.76	This study

Supplementary material

Table S2.2.1. Mean values of sedimentary parameters in the top 3 mm sediment layer of the sampling locations.

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Supplementary material

Multiple corer samples (3 replicates) were collected in the study area at depths between 583 and 1735 m for the analyses of the sedimentary variables in the framework of the project DESEAS (Tselepides et al., 2004). The sediment samples were stored at -22ºC after sectioning into several depth thin layers (the results from the topmost 3 mm are presented in the Table S2.2.1). In the lab, for the analyses of chlorophyll *a* and phaeopigment concentrations, a TURNER 112 fluorometer was used with 90% acetone extractant while phaeopigments were estimated by acidification with 0.1N HCl (Yentsch and Menzel, 1963; Lorenzen and Jeffrey 1980). Chloroplastic pigment equivalents (CPE) were considered as the sum of chlorophyll a and phaeopigment content. Total organic carbon (TOC) and nitrogen (TON) concentrations were measured using a Perkin Elmer CHN 2400 Analyser (Hedges and Stern, 1984). For the grain size analysis, subsampling was carried out using Plexiglas tubes of 4.5 cm internal diameter and analysed according to the method described in Buchanan (1984). See Tselepides et al. (2004) for a description of the methodology for environmental variables.

Table S 2.2.1 Mean values of sedimentary parameters in the top 3 mm sediment layer of the sampling locations. TOC, organic carbon; TON, organic nitrogen; C/N, carbon to nitrogen ratio; Chl.a, clorophyll a; Phaeop., phaeopigments; CPE, chloroplastic pigment equivalent; Chl.a/CPE, ratio of Chl.a to CPE; MD, medium diameter of the sediment; % S&C, percentage of silt and clay. Standard deviations not included.

	Depth	**TOC**	**TON**	**C/N**	**Chla**	**Phaeop**	**CPE**	**Chla/CPE**	**MD**	**S&C**
	(m)	%	%		μg g^{-1}	μg g^{-1}	μg g^{-1}		mm	%
South Balearic Sea	**583**	0.47	0.09	6.0	0.67	1.18	1.29	0.20	0.097	74.5
	814	0.6	0.09	7.9	0.21	0.96	1.17	0.19	0.014	90.8
	1429	0.58	0.08	8.2	0.23	1.17	1.4	0.16	0.016	87.3
East Ionian Sea	**600**	0.6	0.07	10.5	0.12	0.68	0.81	0.15	0.012	98.0
	800	0.74	0.08	11	0.28	1.18	1.46	0.19	0.012	97.8
	1735	0.67	0.09	8.5	0.13	0.66	0.79	0.17	0.012	94.9

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2.3 Biodiversity patterns of crustacean suprabenthic assemblages along an oligotrophic gradient in the bathyal Mediterranean Sea

Almeida, M., Frutos, I., Tecchio, S., Lampadariou, N., Company, J.B., Ramirez-Llodra, E., Cunha, M.R. (published online 2017). Biodiversity patterns of crustacean suprabenthic assemblages along an oligotrophic gradient in the bathyal Mediterranean Sea. Deep-Sea Research I.

Abstract

Crustacean suprabenthic abundance, community structure, α-diversity (both taxonomic and trophic) and β-diversity were studied along a West-East gradient of oligotrophy in the deep Mediterranean Sea. The assemblages were sampled with a suprabenthic sledge in three regions (western, central and eastern basins) at three water depths (1200, 2000 and 3000 m) in May-June 2009. Environmental data were obtained at each sampling location including sediment properties, oceanographic variables near the seafloor and in the water column, and proxies of epipelagic productivity at the surface. Our results, concerning the crustacean component of the suprabenthos, showed complex trends in community structure and biodiversity across different spatial scales (longitudinal, bathymetric, and near-bottom distribution). A decrease in the number of species and abundance, accompanied by changes in the trophic structure of the assemblages were observed from West to East. In the eastern region the assemblages were impoverished in number of trophic guilds and trophic diversity. The West-East oligotrophic gradient was identified as the main driver in community structure as shown by the significant correlation with trophic environmental variables. Differences in community structure across regions were more marked at greater depths, while at the shallower sites assemblages were more similar. Within each basin, abundance, number of species and number of trophic groups decreased with depth, showing high turnover rates between 1200 and 2000 m depths. The small-scale (0-150 cm) vertical distribution of the suprabenthos was interpreted in relation to the species' functional traits (e.g. swimming activity, migratory behaviour, bottom dependence, feeding habits). Bottom-dependent and more mobile components of the suprabenthos were apparently responding differently to the various environmental challenges imposed by the large-scale longitudinal and bathymetric gradients. We propose that the bathyal suprabenthos in the Mediterranean Sea may be essentially modulated by environmental sorting, but while the more mobile faunal component has more efficient dispersal mechanisms, the bottom-dependent component may be affected by limited dispersal. However, this empirical interpretation has still to be proved given the important caveats of our study (e.g. typically low densities of the Mediterranean bathyal suprabenthos; limited number of samples; difficulties in standardization inherent to suprabenthic sampling operations in the deep sea).

2.3.1 Introduction

The relationship between the environment and the distribution of the marine fauna is a fundamental issue in ecology, particularly in the deep sea, the largest biome on Earth with a high biodiversity which remains mostly undescribed (Ramirez-Llodra et al., 2010). Despite the increased number of studies on deep-sea fauna, biodiversity patterns still remain largely unknown (Danovaro et al., 2010 and references therein). Local diversity patterns are often associated with several depth-related changes in the environment including productivity, sediment properties, oxygen availability and catastrophic physical disturbance (Etter and Mullineaux, 2001; Levin et al., 2001; Snelgrove and Smith, 2002). Other environmental gradients (e.g. latitudinal, longitudinal), spatial heterogeneity, dispersal and metapopulation dynamics are also likely to be important in explaining biodiversity patterns at a regional scale (Levin et al., 2001). Both local and regional processes can be responsible for producing spatial patterns in community structure (Witman et al., 2004). A general bathymetric trend of decreasing abundance and biomass for mega- and macrobenthic groups is often explained by the decreased nutrient input with increasing depth and distance from productive coastal areas (Rex et al., 2006). Available organic matter in the deep sea is mostly allochthonous; it depends on the downward flux of surface productivity (Gage and Tyler, 1991) and is also influenced by river inputs and climate-driven oceanographic events (Company et al., 2008). Limited food supply is therefore a major driver of community structure and diversity in the deep sea (Levin et al., 2001; Gage, 2003; Smith et al., 2008), and even more so in oligotrophic environments. The West-East oligotrophy gradient and unique depth-related conditions in the Mediterranean Sea make it particularly interesting to investigate bathyal diversity and distribution patterns at basin scales (Bethoux and Pierre, 1999).

The Mediterranean is a semi-enclosed sea connected westwards to the Atlantic Ocean through the Strait of Gibraltar (approx. 320 m maximum depth). It is formed by two depressions, divided by a narrow channel in the Strait of Sicily (approx. 300 m depth) and is usually classified into three basins: western, central and eastern. Particular features are the constant high temperature below 200-300 m depth, approx. 13-14 ºC (Tyler, 2003; Sardà et al., 2004), and the low productivity rates with a decreasing productivity gradient from West to East (Danovaro et al., 1999). The western region has higher productivity due to the terrestrial and atmospheric inputs and the influence of the Atlantic relatively nutrient-rich waters (Company et al., 2008; Bas, 2009), the eastern region has contrasting extreme oligotrophic conditions and is particularly depleted of phosphorus (Bethoux et al., 1998), while the central Mediterranean presents intermediate values of productivity (Stambler et al., 2014).

The deep-sea benthic communities along the changing trophic conditions in the western, central and eastern Mediterranean basins have been recently documented for meiofauna (Pape et al., 2013a,b), macrofauna (Baldrighi et al., 2014) and megafauna (e.g. Tecchio et al., 2011a, 2011b, 2013) under the scope of a multidisciplinary project (BIOFUN, EuroDEEP-ESF) aiming to understand the linkages between biodiversity patterns and ecosystem functioning in relation to environmental conditions. Deep-sea biodiversity patterns for different taxa, reviewed and compared by Danovaro et al. (2010), suggest that the composition, abundance and community structure are affected by the longitudinal productivity gradient in the Mediterranean basins (Tselepides et al., 2000; Danovaro et al., 2008; Tecchio et al., 2011b). Both primary and secondary production processes taking place at the sea surface are key drivers for controlling the benthic standing stock and structuring the deep-sea food web (Tecchio et al., 2013). Studies on the bathyal Mediterranean suprabenthos are mostly limited to the western region (e.g. Cartes et al., 2003, 2008, 2011) and the information on its distribution patterns and diversity is scarce, especially in the central and eastern basins, and at depths greater than 1000 m.

Suprabenthos is mainly composed of small crustaceans that live in the immediate vicinity of the seafloor, many of which perform (with varying amplitude, intensity and regularity) seasonal or diel vertical migrations into the water column (Brunel et al., 1978; Mees and Jones, 1997). However, most studies on bathyal suprabenthic species report limited or no nocturnal upward migrations (Cartes and Sorbe, 1995; Cartes, 1998, Cartes et al., 2011 Koulouri et al., 2013, Frutos and Sorbe 2014). The suprabenthos is considered as a complex compartment since it comprises a broad assemblage of species related only by their distribution in space and not by phylogeny or exclusively functional attributes (Mees and Jones, 1997). The differing swimming behaviour and bottom dependence of the various taxa results in a stratified distribution of this fauna near the seafloor. The suprabenthos plays an important role in deep-sea trophic webs. It includes predators on meiofauna and zooplankton, filter feeders and surface deposit feeders mobilizing particulate organic matter and detritus at the vicinity of the seafloor (Fanelli et al., 2009). On the other hand, it constitutes the main food source of many fish and decapods, including commercially relevant species (e.g. Carrassón and Cartes, 2002).

The present study provides a detailed quantitative analysis of the deep-sea suprabenthic crustacean assemblages collected along a Trans-Mediterranean gradient of increasing oligotrophy. We hypothesize that abundance, diversity and trophic structure of the suprabenthic crustacean assemblages will change with longitude and depth and strongly depend on the prevailing environmental conditions. The specific aims of the study were: (i) to investigate the longitudinal- and depth-related trends in biodiversity and trophic structure; (ii) to examine the small-scale (0-150 cm above seafloor) vertical patterns of the suprabenthos' near-bottom distribution in relation to these large-scale trends and (iii) to relate the observed patterns with the prevailing environmental conditions.

2.3.2 Material and methods

2.3.2.1 Study area

Three regions in the Mediterranean Sea were sampled: the southern Balearic Sea in the western basin (W), the western Ionian Sea in the central basin (C) and the south of Crete in the eastern basin (E) (Fig. 2.3.1). Across this longitudinal gradient, sites were sampled at approximately 1200 m (1130-1200 m), 2000 m and 3000 m (2850-3335 m) (Fig. 2.3.1; Table 2.3.1) during a multidisciplinary oceanographic cruise aboard the RV Sarmiento de Gamboa (May-June 2009) in the framework of the European Science Foundation funded project BIOFUN (BIOdiversity and ecosystem FUNctioning in contrasting southern European deep-sea environments: from viruses to megafauna, ESF-EuroDeep).

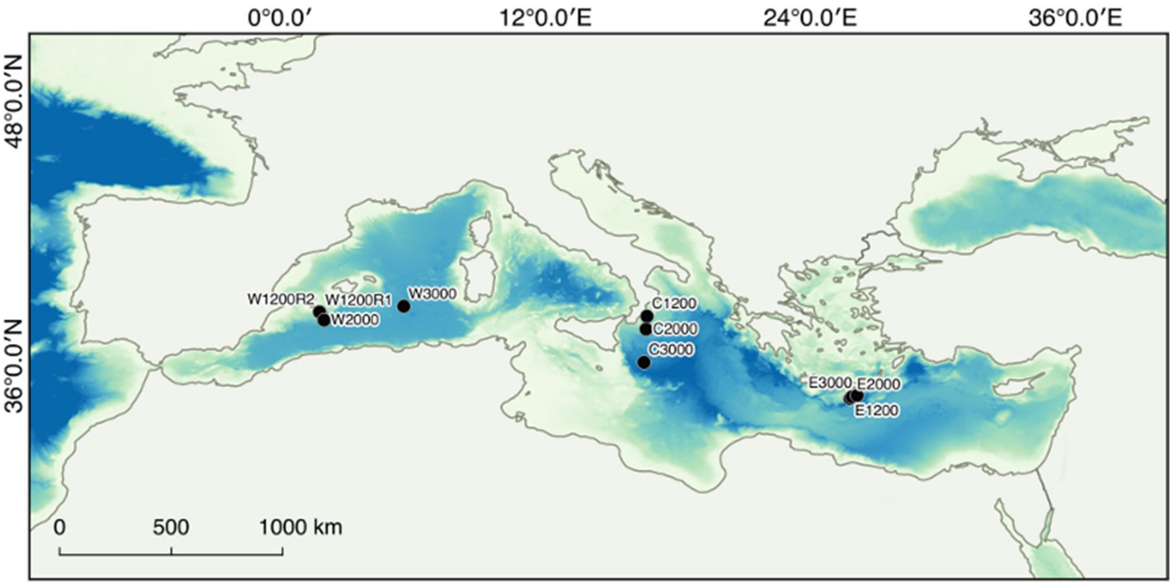

Figure 2.3.1 Location of sites sampled in the Mediterranean Sea at the three study areas. W (western basin, southern Balearic), C (central basin, western Ionian) and E (eastern basin, south of Crete).

Table 2.3.1 Main characteristics of the sampling sites from the three study areas of the Mediterranean Sea. W: western basin (R1 and R2 refer to the two hauls collected at 1200 m), C: central basin, E: eastern basin. 1200, 2000 and 3000 refer to the approximate sampling depth.

Haul code	Site	Date (d/m/y)	Geographical area	Hour[a] (h:m)	Position		Mean Depth(m)	Lenght[b] (m)	Area[c] (m^2)	Volume[d] (m^3)
					N	E				
BF1P2	W1200R1	31/05/09	S Balearic	14:20	38°23.67'	1°49.39'	1195	2039.9	1631.9	652.8
BF1P3	W1200R2	31/05/09	S Balearic	16:49	38°26.12'	1°47.27'	1130	1622.8	1298.2	519.3
BF1P4	W2000	02/06/09	S Balearic	01:29	38°04.13'	1°59.50'	2000	3632.0	2905.6	1162.2
BF1P5	W3000	04/06/09	S Balearic	02:16	38°41.47'	5°35.98'	2850	3494.1	2795.3	1118.1
BF1P6	C1200	08/06/09	West Ionian	05:20	38°14.68'	16°35.89'	1200	2817.7	2254.1	901.7
BF1P7	C2000	08/06/09	West Ionian	18:40	37°39.41'	16°33.50'	2000	3753.4	3002.8	1201.1
BF1P8	C3000	10/06/09	West Ionian	03:54	36°09.25'	16°27.93'	3335	2946.5	2357.2	942.9
BF1P9	E1200	16/06/09	South Crete	02:50	34°31.22'	25°46.97'	1200	3646.3	2917.1	1166.8
BF1P10	E2000	17/06/09	South Crete	03:24	34°34.99'	25°51.81'	2000	3704.0	2963.2	1185.3
BF1P11	E3000	20/06/09	South Crete	02:50	34°39.30'	26°06.14'	2900	3735.8	2988.7	1195.5

a)hour at the beginning of the haul; b)bottom sampled by the sledge during the haul; c)bottom area sampled during the haul; d)volume of water filtered by one net during the haul.

2.3.2.2 Sample collection and processing

The suprabenthic assemblages were sampled at nine sites: W, C and E basins at three depths. Only one sample was taken at each site, except for 1200 m in the W basin, where two hauls were collected. The sampling gear used is a modified version of the Macer-GIROQ sledge (see Cartes et al., 1994 for a full description). Briefly, this gear is composed of three superimposed nets (0.5 mm mesh size; opening of the net: 80 cm width and 40 cm height) which allow quantitative sampling of the fauna in three water layers above the seafloor: 10-50 cm water layer (N1), 55-95 cm water layer (N2) and 100-140 cm water layer (N3). The sledge was equipped with an opening closing-system activated by contact with the seafloor (preventing contamination by pelagic organisms from the water column). The distances hauled were calculated on the basis of the coordinates of the start and end of the haul, which were carried out for ca. 60 min at a speed of approximately 2 knots. Detailed information on each haul is presented in Table 2.3.1.

The collected fauna was sieved through a 500 µm mesh and fixed on board with 10% formalin. In the lab, the samples were sorted to various taxa under a dissecting microscope and kept in 70% alcohol. Organisms were identified at species level, whenever possible, and counted. Some taxa were not yet identified to species level but they were all sorted into putative species and ascribed a codename consistent throughout the samples. Only the crustaceans (Order Malacostraca only) were considered in this study. Thus, copepods, ostracods and all non-crustacean taxonomic groups collected by the gear were excluded: e.g. polychaetes, molluscs, echinoderms, chaetognaths, gelatinosous taxa and demersal fishes. For simplicity, throughout the text, we use suprabenthos as referring to the analysed component. For the multivariate analysis, juveniles and unidentified (damaged) specimens were excluded. The density of each taxon was calculated from the area swept by the sledge on the bottom (haul length x net opening width) and expressed as number of individuals per 100 m^2 for the 10-140 cm water layer (total fauna). Densities were also expressed as individuals per 100 m^3 for the 10-50, 55-95 and 100-140 cm water layers (respectively N1, N2 and N3).

For the collection of environmental data at each location, water column variables near the seafloor, namely benthic temperature (°C), benthic salinity (PSU), benthic turbidity (Formazin turbidity units, FTU) and benthic dissolved oxygen ($mg.l^{-1}$), were obtained using a Seabird 9plus CTD and data processing using SBE data processing software v.7.18d. The values for these water column variables were obtained by averaging five measurements taken along the 5 m above the seafloor. The mean values of the fluorescence data (relative fluorescence units, RFU, obtained also with the CTD) in the 0-150 m depth range were used as a relative indicator of surface primary production. For sediment analyses, a multicorer sample was taken at each location and the top 1 cm was used to determine sediment POC (% of mass) and grain size (% of coarse fraction, >63 µm) (S2.3.1, Supplementary material).

For the estimation of the epipelagic zooplankton biomass at each location, two nets were used to collect plankton from 200 m depth to the surface: a standard WP2 net with a 200 µm mesh for mesozooplankton and a scaled-down version for microzooplankton with a 53 µm mesh size. A remotely-controlled Rectangular Midwater Trawl (RMT) net with 1 mm mesh size was used to retrieve macrozooplankton samples at 140-550 m below the surface (according to the depth of the deep scattering layer visible in the shipboard sonar). On board, the mesozooplankton and microzooplankton samples were sieved, filtered and stored at −20 °C. Once in the laboratory, the filters were freeze-dried for 48 h and weighted. Macrozooplankton samples were sorted into major faunal groups in the laboratory and weighted. All biomasses were standardised by filtered water volume (S1, Supplementary material).

See Tecchio et al (2011b) for a more detailed description of the methodology for environmental variables and zooplankton biomass.

2.3.2.3 Data analysis

The data on each one of the three nets, N1 (10-50 cm), N2 (55-95 cm) and N3 (100-140 cm) were initially kept separately in order to examine the near-bottom vertical distribution of the suprabenthos. Furthermore, the samples were allocated to three geographical categories (W, C, E) and three bathymetric categories (1200 m, 2000 m and 3000 m) used in the multivariate analyses to assess the effect of depth and longitude (West-East gradient) on the biodiversity and structure of the assemblages. Non-metric multidimensional scaling (nMDS) was performed on the Bray–Curtis similarity matrix based on the abundance data (density expressed as ind.100 m^{-3}), after square-root transformation. ANOSIM analysis (one-way ANOSIM) was used to test the statistical significance of differences in the biological assemblages related to the near-bottom vertical distribution, geographical location and depth.

Suprabenthic trophic structure was estimated by allocating each taxon to a trophic guild based on, food source, food type and size and feeding mode (adapted from MacDonald et al., 2010 with information compiled from Cartes, 1998, Madurell et al., 2008; Fanelli et al., 2009). Food source of suprabenthic crustaceans was assigned to one of the following categories: water column/epibenthic (EP), seafloor surface (SR), and sediment subsurface (SS). Food type and size were described as sediment (sed), particulate organic matter (pom), microfauna (mic), meiofauna (mei), macrofauna (mac), phytodetritus (phy), zooplankton (zoo) and fish (fis). Feeding mode included detritus feeders (Dt), suspension/filter feeders (Su), predators (Pr), scavengers (Sc), Suctorial parasites (Sp), grazers (Gr) and omnivorous (Om) (for more details see MacDonald et al., 2010).

Diversity was estimated using number of species, Shannon–Wiener diversity (*H'*, ln-based), Pielou (1969) evenness index (*J'*) and the expected number of species $ES_{(n)}$ for each sampling site (by water layer and for the whole sample). Suprabenthic species were also ranked according to the 10 numerically dominant species per site (by water layer and for the whole sample). Changes in the composition of the suprabenthic assemblages were assessed by species replacement (or turnover) (e.g. Magurran, 2004) across depth and geographical location (by water layer and for the whole sample). The index used was $T= (L+G)/S$; where L is the number of taxa lost, G is the number of taxa gained and S is the pooled number of taxa in the two consecutive depths or areas; T values vary between 0 (no changes in the assemblage; G=0 and L=0) and 1 (complete renovation of the assemblage; L+G=S).

Diversity partitioning was assessed for number of species (S), Hurlbert's expected number of species ($ES_{(30)}$) and Shannon–Wiener index (*H'*) and their equivalents for trophic diversity. The total diversity ($\gamma=\alpha+\beta$) is partitioned into the average diversity within the lowest level of sampling (α) and among sampling levels (β) and therefore β-diversity can be estimated by $\beta= \gamma-\alpha$ (Wagner et al., 2000; Magurran, 2004). To extend the partition across multiple scales (β_1= between water layers, β_2= between bathymetric levels and β_3= between regions) the smallest sample unit for level 1 are individual nets from each sledge sample (α diversity), while for the upper levels sampling units are formed by pooling together the appropriate groups of nested samples. The diversity components are calculated as $\beta_m= \gamma-\alpha_m$ at the highest level and $\beta_i= \gamma-\alpha_{i+1}- \alpha_i$ for each lower level. The additive partition of diversity is $\gamma = \alpha1 + \beta1 + \beta2 + \ldots + \beta m$. The total diversity can therefore be expressed as the percentage contributions of diversity in each hierarchical level (Crist et al., 2003). Partitioning was carried out by weighting each sample according to its respective abundance. Values of α_i were therefore calculated as a weighted average (according to the number of samples pooled).

A distance-based redundancy analysis (dbRDA) was used to visualize the relationship among the samples and in relation to environmental variables. Note that the environmental dataset refers to measurements taken at each location and each location can be associated with one suprabenthic haul (i.e. there are no environmental measurements specifically associated with each water layer of the suprabenthic sledge). The available measurements of pelagic variables (0-200 m microzoopl., 0-200 m mesozoopl., DSL macrozoopl. and fluorescence) were used as proxies of the organic flux to the benthic assemblages. Non-parametric Spearman's rank correlation coefficients were calculated between the set of environmental variables and taxonomic and trophic diversity and abundance of the suprabenthic assemblages (near-bottom and upper water layers) in order to further infer on the putative drivers for the distribution of these assemblages. Significance values for multiple comparisons were adjusted by using the Bonferroni correction (Dunn, 1961) at a significant level of α/m (number of hypotheses tested).

The indices and the multivariate analyses were performed using PRIMER v6 (Clarke and Gorley, 2006) and the correlation coefficient was calculated using GraphPad Prism v.6.0 (GraphPad Software, La Jolla California USA, www.graphpad.com).

2.3.3 Results

A total of 3685 individuals were counted and ascribed to 116 crustacean taxa from which 24 (20.7%) were singletons. The amphipods (gammarideans: 31.8% of total abundance; 36 species and hyperiids: 4.2%; 15 species) were the most abundant and species-rich group. The mysids were the second most abundant group (34.2% of total abundance; 10 species). Cumaceans (10.7%, 22 species) and isopods (8.9%; 13 species) showed intermediate values of abundance and number of species, while euphausiids (6.7%; 6 species) presented similar values of abundance but lower number of species. The decapods (3.0%; 11 species) were less abundant but well represented in terms of number of species. These groups were collected in all samples, except for the sites E3000 and W3000, where cumaceans and decapods, respectively, were absent. The lophogastrids, tanaids and leptostraceans were only represented by one species each (<1% of total abundance).

The pooled number of species was high in W (80 species) and C (81 species) and decreased in E (68 species) and a more marked decrease in the pooled number of species was observed with increasing depth (98 at 1200 m, 69 at 2000 m, 53 at 3000 m) (Table 2.3.2). Overall, 27.6% of the species occurred all along the West-East gradient at all depths and throughout the sampled water column (10-140 cm). The highest values of number of species per site were found at the shallowest depths of each basin, 52 species in the W, 49 in the C and 53 in the E (Table 2.3.2). Total densities decreased gradually with increasing depth in the W (36.5 ind.100m^{-2} to 3.5 ind.100m^{-2}) and C (16.2 ind.100m^{-2} to 10.6 ind.100m^{-2}). In the E the highest value was recorded in the shallowest site (28.2 ind.100m^{-2}) with lower but similar values at 2000 and 3000 m (5.5-7 ind.100m^{-2}).

Table 2.3.2 Abundance and biodiversity (taxonomic and trophic) of suprabenthic crustaceans illustrating the near-bottom vertical distribution and the total assemblage in the sites sampled. W: western basin (R1 and R2 refer to the two hauls collected at 1200 m), C: central basin, E: eastern basin; N1:10-50 cm; N2+N3: 55-140 cm; N: abundance; S: number of species; H': Shannon-Wiener Diversity index (ln-based); J': Pielou evenness index; $ES_{(30)}$ and $ETG_{(30)}$: Hurlbert's expected number of species and trophic groups, respectively.

					Taxonomic				**Trophic**			
Site	**Water layer**	***N***	**Density ind.100m^{-3} / ind.100m^{-2}**		***S***	***H'***	***J'***	**$ES_{(30)}$**	***TG***	***H'***	***J'***	**$ETG_{(30)}$**
W1200R1	N1	493	75.5		47	2.67	0.693	13.0	11	1.69	0.704	6.5
	N2+N3	102	7.8		15	1.45	0.536	7.3	8	0.82	0.395	4.6
	Total	595		36.5	52	2.61	0.660	12.9	12	1.61	0.649	6.5
W1200R2	N1	263	50.6		29	2.56	0.760	13.1	9	1.47	0.668	5.8
	N2+N3	71	6.8		14	1.71	0.648	8.9	5	1.03	0.641	4.4
	Total	334		25.7	35	2.53	0.712	12.9	10	1.44	0.623	5.9
W2000	N1	377	32.4		38	2.78	0.763	13.6	12	1.65	0.666	6.2
	N2+N3	65	2.8		12	1.90	0.765	9.5	6	1.10	0.613	4.5
	Total	442		15.2	42	2.80	0.749	13.6	12	1.61	0.648	6.1
W3000	N1	78	7.0		21	2.78	0.912	15.2	9	1.87	0.850	7.1
	N2+N3	21	0.9		5	1.47	0.912	5.0	4	1.17	0.845	4.0
	Total	99		3.5	23	2.92	0.933	16.4	9	1.84	0.837	7.1
C1200	N1	261	28.9		34	2.54	0.721	12.5	11	1.86	0.776	7.8
	N2+N3	104	5.8		35	3.01	0.848	17.3	11	1.73	0.723	7.7
	Total	365		16.2	49	2.82	0.724	14.1	13	1.85	0.721	7.7
C2000	N1	363	30.2		35	2.62	0.738	12.9	10	1.57	0.683	6.0
	N2+N3	47	2.0		12	2.09	0.841	10.2	4	1.20	0.866	4.0
	Total	410		13.7	39	2.71	0.739	13.4	10	1.59	0.690	6.1
C3000	N1	199	21.1		26	2.60	0.799	12.9	9	1.65	0.752	6.3
	N2+N3	51	2.7		18	2.63	0.908	15.6	5	1.07	0.666	4.2
	Total	250		10.6	33	2.88	0.825	14.8	9	1.60	0.730	6.1
E1200	N1	742	63.6		45	2.49	0.654	11.5	11	1.26	0.524	5.1
	N2+N3	81	3.5		22	2.63	0.851	14.2	4	0.99	0.713	3.4
	Total	823		28.2	53	2.66	0.670	12.6	11	1.27	0.531	5.1
E2000	N1	119	10.0		17	2.06	0.728	9.5	8	1.29	0.620	5.1
	N2+N3	43	1.8		13	2.21	0.862	11.5	3	0.77	0.703	2.8
	Total	162		5.5	26	2.55	0.782	12.4	8	1.38	0.661	4.9
E3000	N1	152	12.7		14	1.48	0.561	7.3	6	0.74	0.415	3.5
	N2+N3	53	2.2		19	2.54	0.862	14.9	4	1.02	0.739	3.8
	Total	205		6.9	29	2.11	0.627	10.9	7	0.99	0.511	4.4
1200		2117			98			14.9	14			6.9
2000		1014			69			15.8	13			6.4
3000		554			53			15.8	12			6.5
W		1470			80			14.8	14			6.5
C		1025			81			16.1	13			7.3
E		1190			68			14.5	11			5.7
All					116			16.3	14			6.9

2.3.3.1 Multivariate analysis

The MDS plot (Fig. 2.3.2) shows that the strongest pattern in the suprabenthic assemblages is the near-bottom vertical distribution with a clear segregation of the near-bottom component of the assemblages (N1, right side of the plot). The samples from the middle (N2) and upper (N3) nets show a high dispersion in the plot probably owing to the lower number of species and particularly low densities yielded by these components (see also Figs. 2.3.3 and 2.3.4). The assemblages from W and E also occupy well-defined positions in the plot (top and bottom, respectively) whereas the samples from C are interspersed with the samples from the two other areas (C3000 closer to E samples; C1200 and C2000 closer to W samples). The separation of the sites by bathymetric levels is less clear. However, the ANOSIM tests (Table 2.3.3) indicate significant differences in the community structure for the three factors, but with decreasing significance values for vertical distribution ("net"), geographical location ("area") and depth (global R=0.494, P=0.1%; R=0.149, P=1.9%; R=0.125, P=4.1%, respectively). W1200 and C2000 samples were taken during daytime (all other during nigh-time) but this factor had no apparent relation with the distribution of samples in the MDS plot and was not relevant in the analysis (R=0.021, P=32.8%). Pairwise comparisons showed significant differences between N1 and the two other nets for near-bottom vertical distribution, between W and E for geographical location, and between 1200 m and 3000 m for depth (Table 2.3.3). Because the densities in N2 and N3 were always very low and pairwise comparisons showed no significant differences between them, the composition and structure of the suprabenthic assemblages have been analysed and represented graphically always considering only two components of the vertical distribution of the assemblages: near-bottom water layer (N1: 10-50 cm) and upper water layer (N2+N3: 55-140 cm).

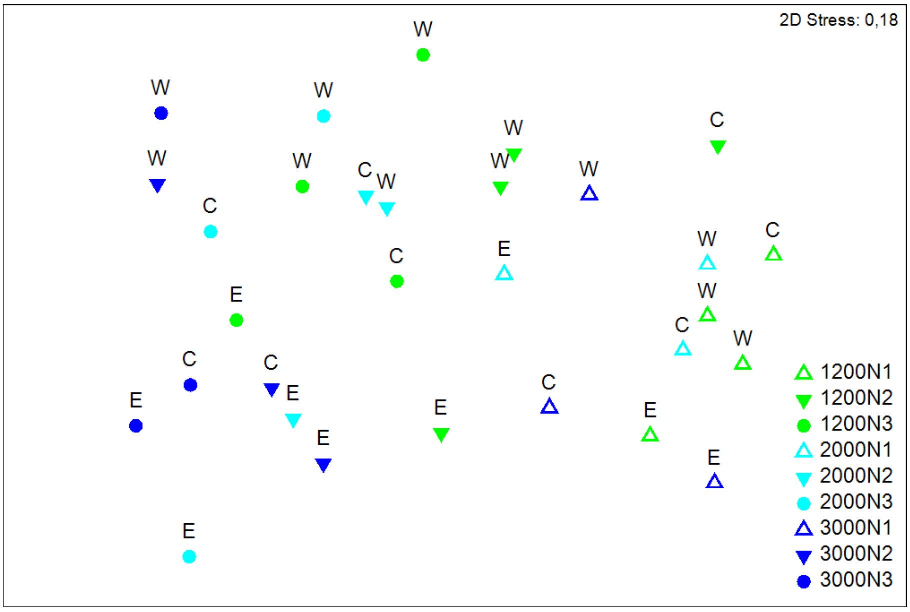

Figure 2.3.2 MDS (multidimensional scaling) 2D ordination plot based on abundance data (ind.100 m^{-3}) of the suprabenthic assemblages from the Mediterranean Sea. W: western basin, C: central basin, E: eastern basin. N1: 10–50 cm (near-bottom) water layer, N2: 55–95 cm water layer, N3: 100–140 cm water layer. 1200, 2000 and 3000 are the sampling depths. Different symbols indicate different water layers (open triangle, N1: 10-50 cm near-bottom; full inverted triangle, N2: 55-95 cm; circle, N3: 100-140 cm) and the different colours indicate different depths (1200, 2000 and 3000 m).

Table 2.3.3 Results of the one way ANOSIM global and pairwise tests. ANOSIM test 1 factor “net” (near-bottom vertical distribution); ANOSIM test 2: factor “area” (geographic location); ANOSIM test 3: factor “depth”. W: western basin, C: central basin, E: eastern basin. N1: 10–50 cm (near-bottom) water layer, N2: 55–95 cm water layer, N3: 100–140 cm water layer. 1200, 2000 and 3000 are the sampling depths.

	Sample Statistic	**Permutation used**	**Significant statistics**	**P**
Anosim test 1: net				
Global value	0.494	999	0	0.1**
Pairwise tests				
N1, N2	0.592	999	0	0.1**
N1, N3	0.785	999	0	0.1**
N2, N3	0.078	999	116	11.7 ns
Anosim test 2: area				
Global value	0.149	999	18	1.9*
Pairwise tests				
W, C	0.096	999	106	10.7 ns
W, E	0.308	999	10	1.1*
C, E	-0,011	999	460	46.1 ns

	Sample Statistic	Permutation used	Significant statistics	P
Anosim test 3: depth				
Global value	0.125	999	40	4.1*
Pairwise tests				
1200, 2000	0.091	999	103	10.4 ns
1200, 3000	0.267	999	6	0.7**
2000, 3000	-0,018	999	506	50.7 ns

* significant; **very significant; ns: not significant.

2.3.3.2 Trends in assemblage composition (taxonomic and trophic groups) and abundance

The suprabenthic assemblages showed a vertical distribution characterised by a decrease both in number of species and density from the near-bottom to the upper water layer (especially from N1 to N2). From a total of 116 species, 51 occurred only in the near-bottom layer, 14 were found only in the upper layers and 51 occurred throughout the sampled water column. Only few species (14) were never found in the near-bottom layer. The gammaridean amphipods were the most species-rich taxa near-bottom (N1) and at 1200 m (maximum of 15 to 17 species per site), although they also occurred in the upper water layer (N2+N3). Cumacean and isopod species were frequent near-bottom, especially at 1200 and 2000 m (6 to 15 species), but were almost absent in the upper water layer. Mysid species were distributed vertically in both water layers although more species occurred at near-bottom (maximum 3-7 species); the number of decapod and euphausiid species was similar in both water layers (ca. 4 species). The number of hyperiid species increased two times from the near-bottom to the upper layer in all E sites (from 2-4 to 5-8 species) and in C3000 (5 to 8 species) (Fig. 2.3.3). In summary, gammaridean amphipods, cumaceans and isopods which have typically a closer interaction with the sediment, showed higher number of species in the near-bottom (with the exception of the site C1200) while highly mobile taxa (hyperid amphipods, shrimps and euphausiids) showed higher number of species (and a much higher relative contribution to the total number of species) in the upper water layer. Overall, number of species decreased from the near-bottom to the upper water layer and from the shallower to the deeper sites (except for C and E at 3000 m, Fig. 2.3.3). Along the West-East gradient a decrease in number of species was observed in the near-bottom, while it slightly increased in the upper water layer.

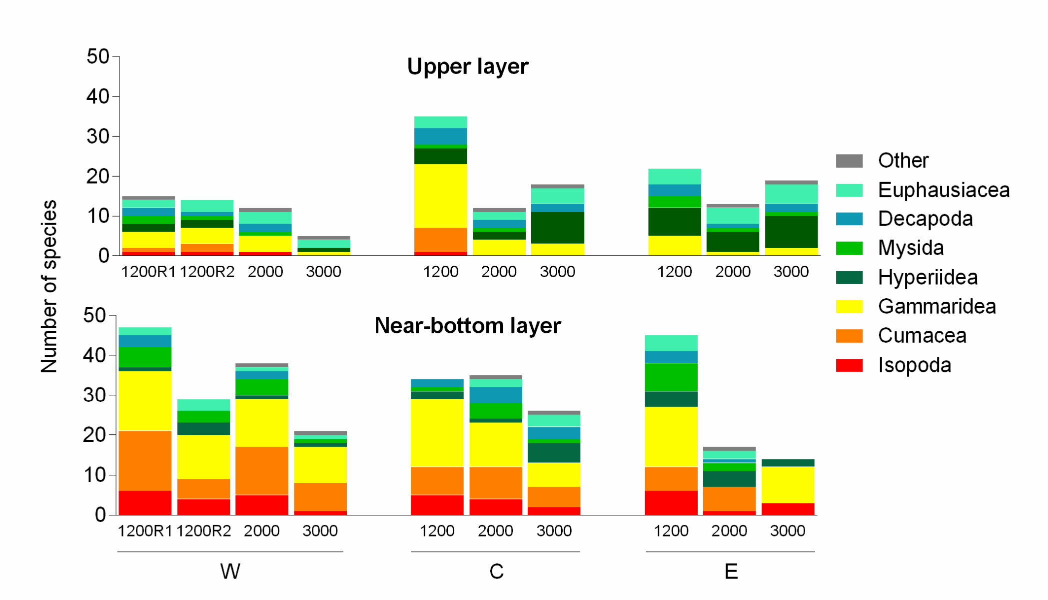

Figure 2.3.3 Number of species of the major taxonomic groups of suprabenthos from each haul taken in the Mediterranean Sea. Near-bottom layer (N1: 10-50 cm); upper layer (N2+N3: 55-140 cm); W: western basin; C: central basin; E: eastern basin. Other: Tanaidacea, Lophogastrida and Leptostraca.

Greater and more consistent differences in the near-bottom vertical distribution were observed in terms of densities of the various crustacean groups (Fig. 2.3.4). The observed densities were generally low; in the near-bottom they ranged from 7.0 to 75.5 ind.100 m^{-3} (W3000 and W1200, respectively), and in the upper layer from 0.9 to 7.8 ind.100 m^{-3} (W3000 and W1200, respectively). The most abundant groups were the mysids, gammaridean amphipods, and cumaceans (maxima of 37.6 in EM1200N1, 27.6 and 10.4 ind.100 m^{-3} in WM1200R1N1, respectively; Fig. 2.3.4). In all the other groups the maximum density was below 8.5 ind.100 m^{-3}. Overall, densities were much lower in the upper water layer (>80% of the fauna occurred in N1), decreased with increasing depth and also from the western to the eastern basin (although more notably in the lower water layer; Fig. 2.3.4). These trends were determined mostly by variations in the abundance of mysids and by the very low densities of gammaridean amphipods, cumaceans and isopods in the upper water layer; decapods, euphausiids and hyperiids were less abundant in the near-bottom (N1) at some sites, but the opposite trend was found in most species (Figs. 2.3.4 and S2.3.2, Supplementary material). In the upper water layer at E sites across all depths and at 3000 m sites across all geographic locations a noticeable increase in the relative contribution of hyperiid amphipods was accompanied by a concurrent decrease of mysids (obvious when relative contributions are plotted; see Fig. S2.3.2, Supplementary material).

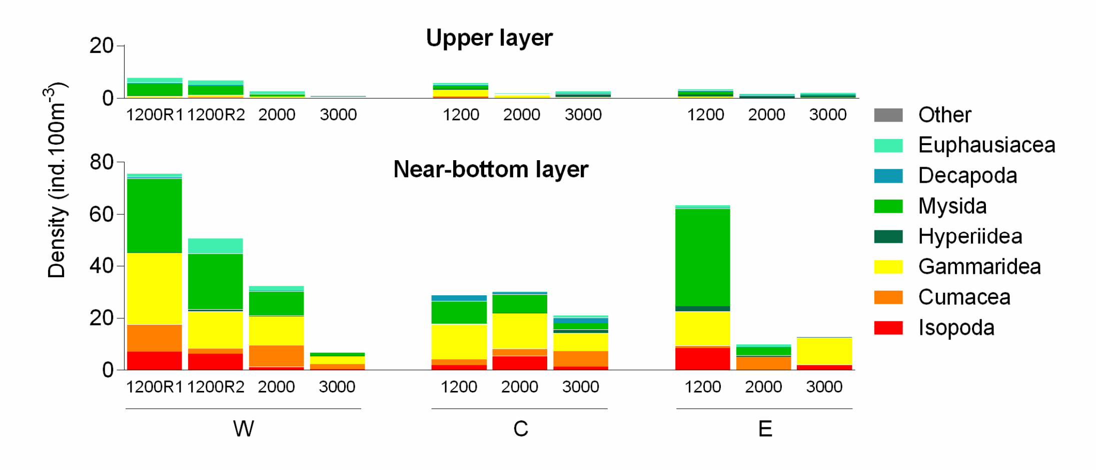

Figure 2.3.4 Density (ind.100 m^{-3}) of the major taxonomic groups of suprabenthos from each haul taken inthe Mediterranean Sea. Near-bottom layer (N1: 10-50 cm); upper layer (N2+N3: 55-140 cm); W: western basin; C: central basin; E: eastern basin. Other: Tanaidacea, Lophogastrida and Leptostraca.

The relative contribution of the 10 dominant species (Table S2.3.3, Supplementary material) at each site and water layer illustrates the importance of widespread species: the vast majority of the dominant species in the suprabenthos occurred throughout the West-East gradient, at all depths and in both water layers; changes in community structure were mainly due to fluctuations in the dominance of these species. For instance, the two most abundant species, the mysid *Boreomysis arctica* and the amphipod *Rhachotropis caeca,* showed decreasing contributions from W to E and from 1200 to 3000 m. In the near-bottom the assemblage showed more specificity in the way that some dominant species only occurred in this water layer. For instance, *Munnopsurus atlanticus* was the most abundant isopod, ranked within the 5 dominant species in most sites but only in the near-bottom water layer. A similar trend was observed for the amphipod *Mediterexis mimonectes,* the mysid *Parerythrops lobiancoi* and the cumacean *Procampylaspis armata*. On the other hand, the upper water layer was always dominated by widespread species but with more marked changes in dominance especially towards E and with increasing depth. For instance, the contributions of euphausiids and hyperiids were consistently higher in the upper layer but the euphausiids *Nematoscelis megalops* and *Euphausia krohnii* were dominant in W and C, while the hyperiid cf. *Hyperia* sp. was dominant in C and E, and the euphausiid *Euphausia hemiggiba* in E.

The taxa found in this study were ascribed to 14 trophic guilds. The fauna common to both water layers was mainly composed by species preying on zooplankton (e.g. *Rhachotropis* spp. and euphausiid *N. megalops*) and filter feeders feeding on phytodetritus (e.g. euphausiids and mysids, particularly *B. arctica*) from the water column. Surface and subsurface grazers on microbiota (e.g. isopod *M. atlanticus*) and predators on meiofauna (*Campylaspis* spp. and *Procampylaspis* spp.) were common in the near-bottom layer. Zooplankton predators became more important in the upper water layer with increasing depth (for instance in the site E3000, mainly due to the increase of the amphipod *R. caeca*) (Fig. 2.3.5). The relative contribution of predators on meiofauna clearly decreased from W to E and from shallower to deeper sites while the contribution of predators on zooplankton increased with increasing depth.

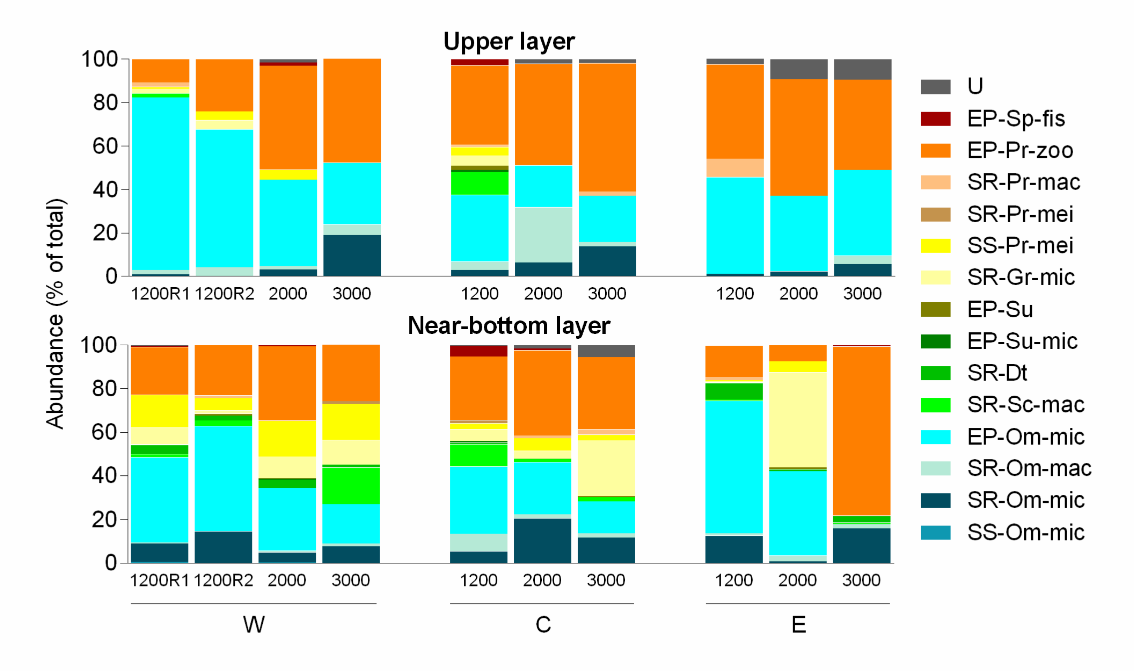

Figure 2.3.5 Relative abundance (%) of the trophic groups in the suprabenthos from each haul taken in the Mediterranean Sea. Near-bottom layer (N1: 10-50 cm); upper layer (N2+N3: 55-140 cm); W: western basin; C: central basin; E: eastern basin; EP: water column; SR: seafloor surface; SS: sediment subsurface; mic: microfauna; mei: meiofauna; mac: macrofauna; zoo: zooplankton; fis: fish; Dt: detritus feeder; Su: suspension/filter feeder; Pr: predator; Sc: scavenger; Sp: sectorial parasite; Gr: grazer; Om: omnivorous; U: unknown.

2.3.3.3 Biodiversity indices

Contrarily to the number of species, biodiversity indices of the suprabenthic assemblage taken as a whole did not show clear patterns in relation to geographical location or depth (Table 2.3.2). However, when the two water layers are considered separately, complex longitudinal and bathymetric patterns are revealed (Table 2.3.2, Fig. 2.3.6). As mentioned before, the number of species decreased in general from W to E in the near-bottom water layer while it increased in the upper layer.

In the W (left column of Fig. 2.3.6) the near-bottom layer always showed higher diversity (S, H, $ES_{(30)}$) than the upper water layer. The decrease in the number of species with increasing depth (Fig. 2.3.6A, left) was accompanied by a clear increase in evenness (Fig. 2.3.6C, left) which resulted in rather similar H’ values (Fig. 2.3.6B, left) at all depths and even increased values of $ES_{(30)}$ with depth (Fig. 2.3.6D, especially in the upper layer). In the E (right column of Fig. 2.3.6) the increase in evenness with depth (Fig. 2.3.6C, right) was not observed and therefore the bathymetric trend in species richness (Fig. 2.3.6A, right) was reflected in H’ and $ES_{(30)}$ (Fig. 2.3.6B and D, right). However, because evenness was substantially lower in the near-bottom layer (Fig. 2.3.6C, right) there was an inversion in the relative values of the two layers: observed S values (Fig. 2.3.6A, right) were higher in the near-bottom while H’ and $ES_{(30)}$ values (Fig. 2.3.6B and D, right) were always higher in the upper layer. Biodiversity patterns in C (Fig. 2.3.6, center column) were less clear and somehow intermediate between the two other regions. The differences between the W and E transects were more obvious at the greatest depth (3000 m), particularly in the near-bottom layer.

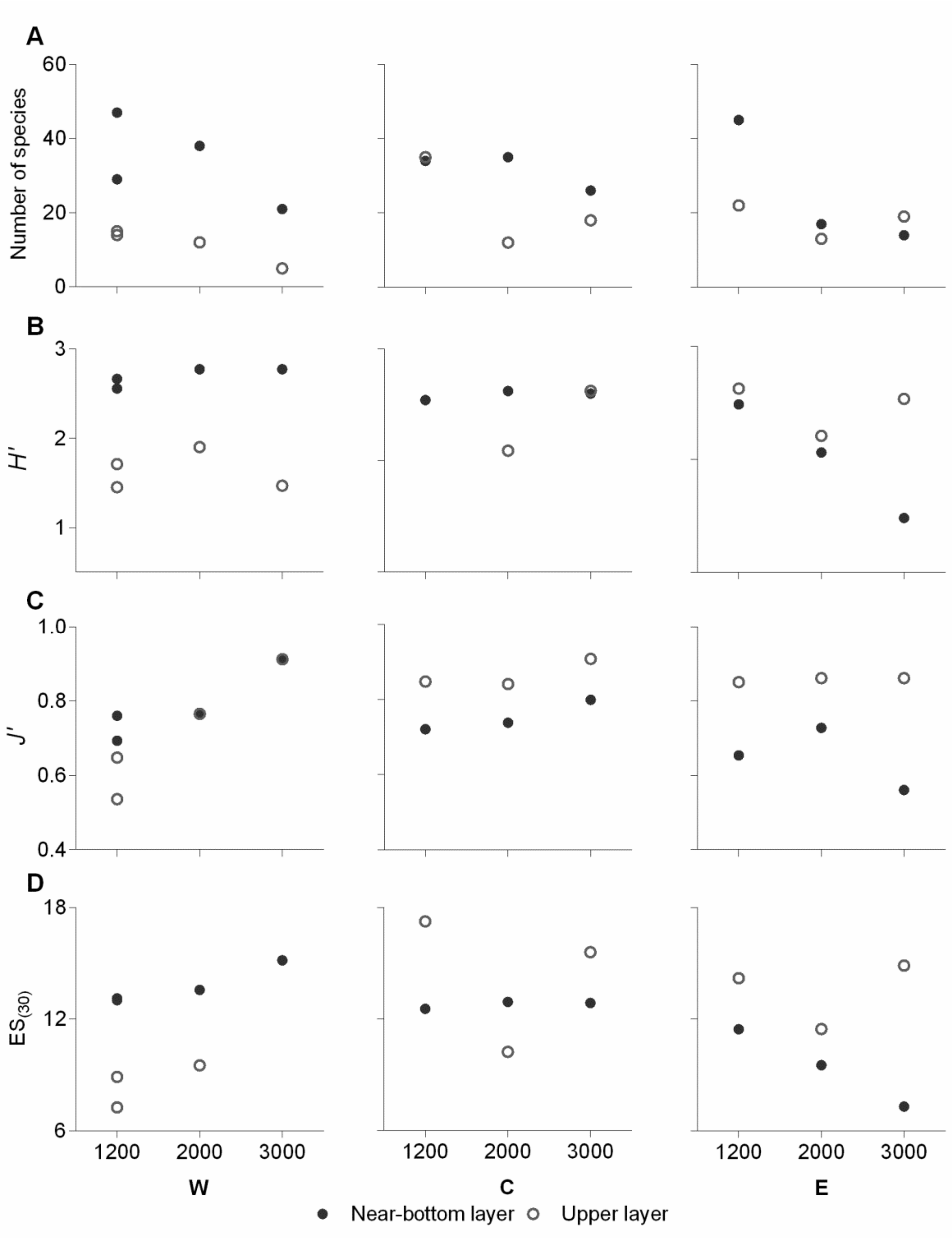

Figure 2.3.6 Biodiversity of the suprabenthic assemblages from the Mediterranean Sea. A: Number of species; B: Shannon-Wiener diversity index (H', ln-based); C: Pielou evenness index (J'); D: Hurlbert's expected number of species ($ES_{(30)}$); W: western basin; C: central basin; E: eastern basin. Full symbols: near-bottom layer (N1: 10-50 cm); Open symbols: upper layer (N2+N3: 55-140 cm).

Patterns of α-diversity are also illustrated by the rarefaction curves (Fig. 2.3.7) and confirmed the same trends: i) overall higher diversity in W, with higher rarefaction values in the near-bottom than in the upper water layer, and the curves for each water layer close together or overlapping; ii) overall lower diversity in E, with lower rarefaction values in the near-bottom than in the upper water layer, and an obvious bathymetric trend of decreasing diversity revealed by the clearly separated curves of the near-bottom water layer; iii) diversity trends in C appearing as intermediate between the two other regions. The steepness of the rarefaction curves, especially for the upper water layers and/or at the greater depth, suggests that the sampling effort was probably not sufficient to assess the full biodiversity of the suprabenthos.

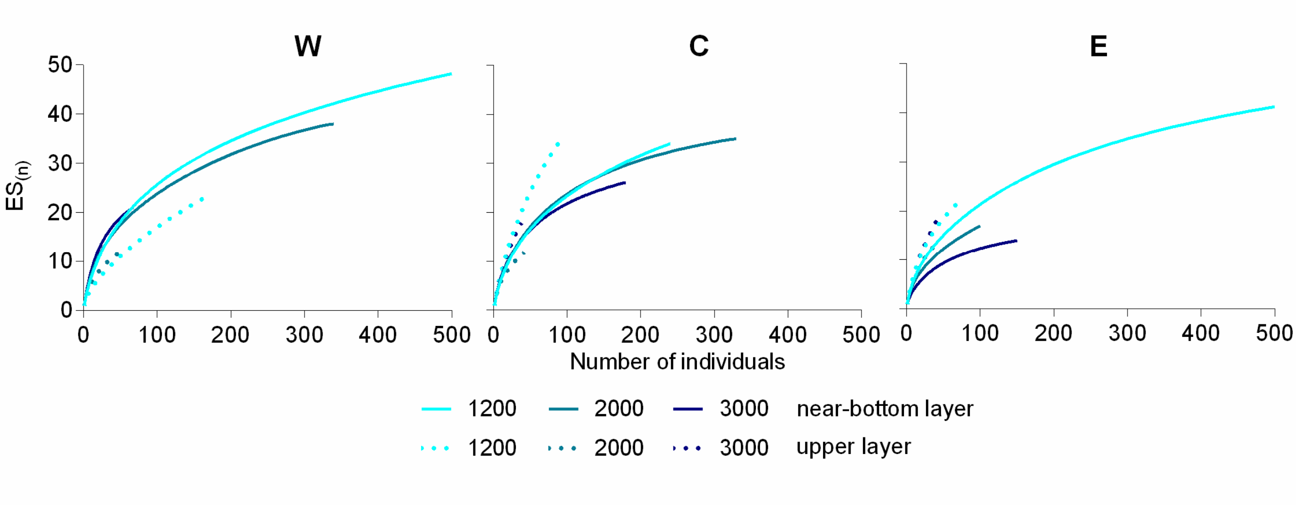

Figure 2.3.7 Rarefaction curves (Hurlbert's expected number of species) of the suprabenthic assemblages from the Mediterranean Sea. Comparison of the two water layers, near-bottom layer (N1: 10-50 cm) and upper layer (N2+N3: 55-140 cm) at 1200, 2000 and 3000 m in the western, central and eastern basins (W, C and E, respectively).

Overall, trophic diversity showed consistently higher values in the near-bottom than in the upper water layer. Overall, trophic diversity values (number of trophic groups, H', J' and $ES_{(30)}$) decreased in the E region. Except for the already mentioned general decrease in the number of trophic groups with increasing depth, there are no other consistent bathymetric trends in trophic diversity (Table 2.3.2).

The β-diversity was assessed by turnover values and showed a dynamic pattern both for bathymetric levels and regions. In most cases, turnover was higher in the upper water layer (except for the transition 2000-3000 m) than in the near-bottom. Across depth, the renewal of species increased in the near-bottom from 1200-2000 m to 2000-3000 m while it decreased in the upper layer (N1: 50.5%, N2+N3: 70.5% at 1200-2000 m; N1: 60.5%, N2+N3: 42.4% at 2000-3000 m). Important to understand turnover is that the suprabenthic assemblage at the shallower depth included 74.5% of the species that occurred exclusively at the near-bottom, 78.6% of the ones occurring exclusively in the upper layer and 96.0% of the ones occurring in both layers. Therefore, bathymetric turnover is determined vastly by losses of species with increasing depth (especially in the transition from 1200 to 2000 m). Along the longitudinal gradient, turnover also showed opposite trends in the two water layers increasing in the near-bottom and decreasing in the upper layer from W-C to C-E (N1: 50.5%, N2+N3: 69.0% at W-C; N1: 54.0%, N2+N3: 58.9% at C-E). Noteworthy is that the assemblage in the W included 70.6% of the species that occurred exclusively at the near-bottom, and 78.0% of the ones occurring in both layers but only 35.7% of the ones occurring exclusively in the upper layer. Therefore, longitudinal turnover is determined mostly by losses in number of species from W to E, but with an important component of new records especially in the upper layer and in the transition from W to C.

The partitioning of biodiversity (Fig. 2.3.8) shows that, at the very small spatial scale (α-diversity - a single net within a single site), the suprabenthic assemblage represented in average only 29% of the total number of species, but much more in terms of number of trophic groups (TG: 66%). The contribution of α-diversity is lower in terms of number of species because even at this small spatial scale most trophic guilds are represented by the species present. For indices related to community structure (H' and $ES_{(30)}$), α-diversity makes most of the contribution to the global observed biodiversity indicating that the structure of suprabenthic assemblages (both taxonomic and trophic) is also well represented at small spatial scales. As for β-diversity, most of the contribution is related to depth (β2), followed by region (β3) and then by the near-bottom vertical distribution (β1), except for number of species where the highest contribution to β-diversity is related to differences between regions (β3).

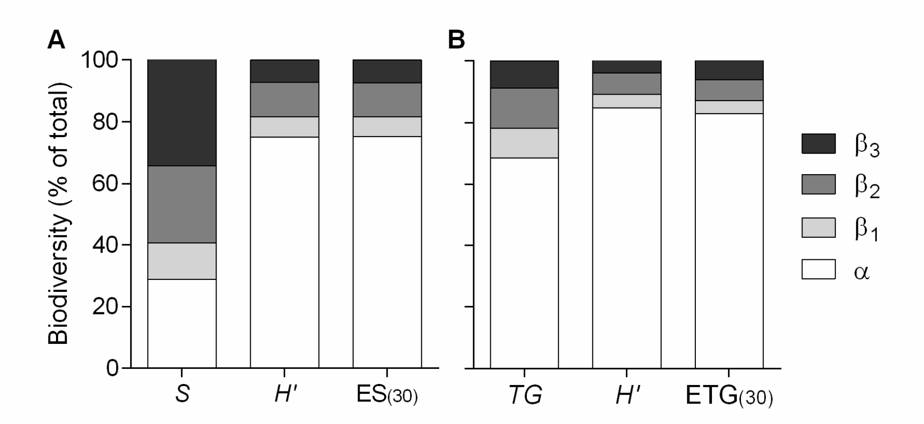

Figure 2.3.8 Partition of taxonomic (left, A) and trophic (right, B) biodiversity. S: number of species; H’: Shannon-Wiener diversity (ln-based); $ES_{(30)}$: Hurlbert’s expected number of species per 30 individuals; TG: number of trophic groups; $ETG_{(30)}$: Hurlbert´s expected number of trophic groups per 30 individuals; α: α-diversity at water layer sampling level; β1: β-diversity between water layers (within site); β2: β-diversity between different bathymetric levels (within region); β3: β-diversity between regions.

2.3.3.4 Suprabenthic assemblages in relation to environmental variables

The dbRDA plot (Fig. 2.3.9) shows the environmental variables potentially driving the changes in community structure across regions and depth. This approach identified the proxies of surface productivity (zooplankton biomasses and fluorescence) as potential drivers for the differences between W and E (Fig. 2.3.9, across the y-axis), and sediment POC best related to the differences between shallower and greater depths (Fig. 2.3.9, from top-right to bottom-left). In C and E at deeper areas, benthic temperature, salinity and sediment grain size are also important variables. However, the % of total variation in composition explained by the analysis is rather low (ca. 30% for the x-axis and 20% for the y-axis).

The nonparametric correlations between the biological data and the measured environmental variables presented in Table 2.3.4 were calculated separately for each of the two water layers in each sampling site (the environmental variables are presented in detail by Tecchio et al., 2011b).

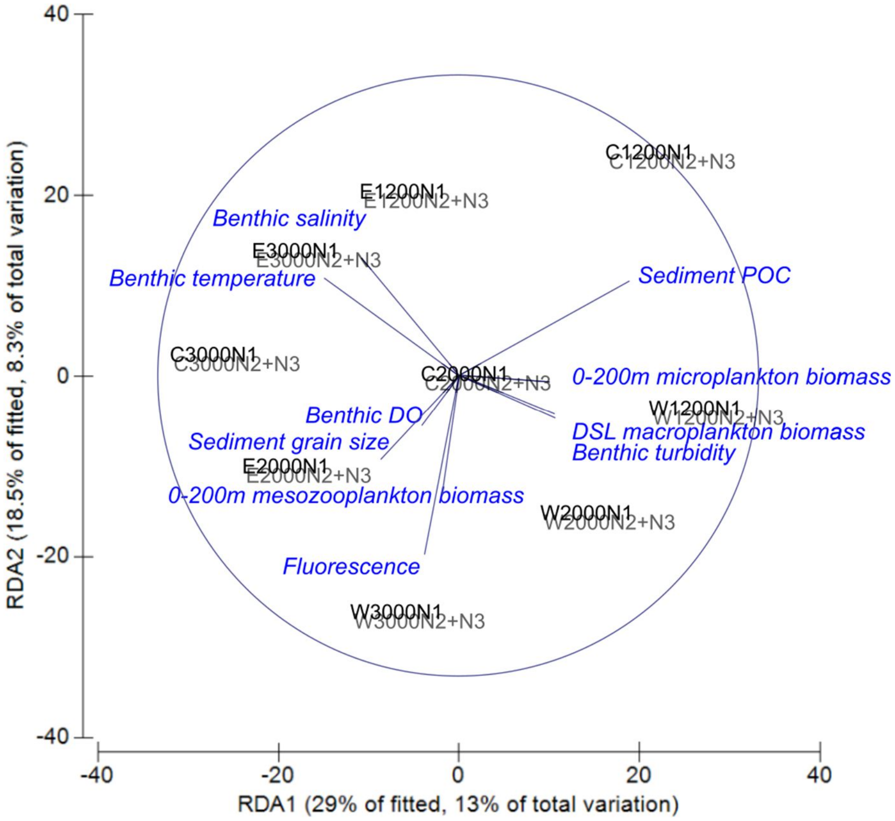

Figure 2.3.9 dbRDA plot for the reduced model of spatial variation in suprabenthic community structure in relationship to environmental variables. W: western basin; C: central basin; E: eastern basin. Note: Note: because there are no environmental measurements specifically associated with each water layer - only to each location - the two water layers (N1 and N2+N3) in each site appear overlapping in the plot.

Densities were only significantly correlated with depth both for the upper and near-bottom water layers. The diversity indices in the near-bottom layer were negatively correlated with longitude and positively correlated with primary productivity at the surface (RFU). Trophic structure (TG) was also positively correlated with particulate organic carbon in the sediment reflecting the importance of productivity fluxes and food availability for the near-bottom assemblage. Noteworthy is that the assemblages in the upper and in the near-bottom layers yield significant correlations often with the same environmental variables, but in opposite ways (negatively *vs.* positively or vice versa). This reflects the contrasting trends in biodiversity and community structure observed in the two water layers both across depth and along the West-East gradient. Note that the most significant correlations (that hold on after the Bonferroni correction) involve mostly the near-bottom assemblage.

Table 2.3.4 Spearman rank correlations between environmental variables and the abundance and biodiversity of suprabenthic assemblages in the two water layers. Significant values ($p<0.05$) are marked in bold with *, significant values after applying the Bonferroni correction ($p<0.041$) are marked with ^{*b}. Dens: density (ind.100 m^{-3}); S: number of species; $ES_{(30):}$ Hulbert's expected number of species per 30 individuals; H': Shannon-Wiener diversity index (ln-based); N1: 10-50 cm near-bottom layer; N2+N3: 55-140 cm upper layer; Benthic temp: temperature (ºC); Benthic sal: salinity in PSU; Benthic DO: dissolved oxygen ($mg.l^{-1}$); Benthic turbidity in FTU (formazin turbidity units); Grain size: sediment grain size (%coarse); Sed POC: sediment particulate organic carbon (% of mass); micropl.: microzooplankton biomass ($mg.m^{-3}$); mesopl.: mesozooplankton biomass ($mg.m^{-3}$); DSL macropl.: macrozooplankton biomass in the deep scattering layer ($g.100\ m^{-3}$); RFU: relative fluorescence units (proxy for surface primary production).

	Benthic Temp.	Benthic Sal.	Benthic DO	Benthic Turbidity	Grain size	Sed. POC	0-200 m micropl.	0-200 m mesopl.	DSL macropl.	RFU	Depth	Long
Dens N1	-0.529	-0.183	-0.402	0.543	-0.456	0.517	0.261	-0.407	0.427	-0.128	**-0.777**^{*b}	-0.467
Dens N2+N3	-0.523	-0.195	-0.378	0.561	-0.547	0.474	0.389	-0.438	0.524	-0.109	**-0.790**^{*b}	-0.467
S N1	-0.535	-0.208	-0.183	0.5	-0.450	0.632	0.28	-0.085	0.384	-0.073	**-0.687***	-0.455
S N2+N3	0.335	0.593	-0.364	0.012	-0.207	0.03	-0.378	-0.280	-0.275	-0.610	-0.380	0.413
$ES_{(30)}$ N1	**-0.742***	**-0.900**^{*b}	0.427	0.335	-0.097	0.377	**0.644***	0.073	0.628	**0.742***	-0.019	**-0.879**^{*b}
$ES_{(30)}$ N2+N3	**0.729***	**0.736***	0.037	-0.427	-0.195	-0.073	-0.547	0.255	-0.610	-0.535	0.058	**0.673***
H' N1	-0.584	**-0.824**^{*b}	0.567	0.201	-0.097	0.353	0.511	0.195	0.47	**0.729***	0.109	**-0.758***
H' N2+N3	**0.699***	**0.824***	-0.061	-0.378	-0.091	-0.043	-0.614	0.274	**-0.659***	**-0.638***	-0.026	**0.709***
J'N1	-0.176	-0.598	**0.677***	-0.152	0.018	-0.043	0.274	0.322	0.104	**0.711***	0.405	-0.552
J'N2+N3	**0.717***	0.39	0.305	**-0.659***	0.62	**-0.681***	-0.62	0.195	**-0.750***	0	**0.726***	0.539
TGN1	-0.517	-0.219	-0.006	0.344	-0.418	**0.729***	0.405	0.268	0.4	0.031	**-0.573***	-0.404
TGN2+N3	-0.519	-0.453	0.193	0.369	**0.620***	0.626	0.582	0.047	0.587	0.249	-0.445	-0.558
ETG$_{(30)}$N1	-0.419	-0.485	0.518	0.335	-0.395	0.468	0.407	0.261	0.39	0.322	-0.116	-0.503
ETG$_{(30)}$N2+N3	-0.626	**-0.610***	0.305	0.439	-0.614	**0.650***	**0.699***	0.103	**0.701***	0.371	-0.366	**-0.661***
H'TGN1	-0.505	-0.598	0.524	0.311	-0.286	0.419	0.541	0.334	0.482	0.456	-0.026	-0.552
H'TGN2+N3	-0.122	-0.264	**0.738***	0.079	-0.377	0.632	0.158	0.608	0.152	0.182	0.148	-0.164
J'TGN1	-0.298	-0.485	0.616	0.311	-0.359	0.286	0.274	0.188	0.274	0.334	0.051	-0.479
J'TGN2+N3	0.419	0.371	0.305	-0.122	0.188	0.03	-0.517	0.31	-0.415	-0.347	0.398	0.564

* $p<0.05$;^{*b} $p<0.041$ (Bonferroni correction)

2.3.4 Discussion

2.3.4.1 Longitudinal and bathymetric trends in abundance, community and trophic structure

Biogeographic trends in deep-sea fauna result from the interaction of ecological and evolutionary processes operating at various spatial and temporal scales (Levin et al., 2001). Bathymetric trends in diversity are often closely related with nutrient input to the seafloor (Gage and Tyler, 1991; Gage, 2003) but many other drivers such as the geologic history, physiography, oceanography, habitat heterogeneity, biotic interactions and metapopulation dynamics determine local and regional deep-sea diversity patterns (Levin et al., 2001; Leibold et al., 2004; Emig and Geistdoerfer, 2004; Coll et al., 2010). The deep-sea Mediterranean fauna is often considered as an impoverished subset of the NE Atlantic fauna that has been shaped by historic events such as the Messinian salinity crisis and Quaternary climate changes (Bouchet and Taviani, 1992; Emig and Geistdoerfer, 2004; Coll et al., 2010). Topography (e.g. the Gibraltar and Sicily straits), oceanographic features (i.e. the deep-water homeothermy and high salinity) and the West-East gradient of oligotrophy, constitute vertical and longitudinal barriers to the colonization and successful establishment of deep-sea Mediterranean fauna (Emig and Geistdoerfer, 2004) wich is characterised by low endemism and a relatively low number of mostly eurybathic species, further decreasing from West to East (Bellan-Santini, 1990; Bouchet and Taviani, 1992; Coll et al., 2010).

Our results show that both the abundance and number of species of the Mediterranean suprabenthic assemblages are lower than the ones found in the NE Atlantic at comparable depths (Elizalde et al., 1993; Dauvin et al., 1995; Marquiegui and Sorbe, 1999; Sorbe, 1999; Frutos and Sorbe, 2014). The reported number of species (including also fishes and pycnogonids) varies between 63 to 116 in studies from the NE Atlantic (Elizalde et al., 1993; Marquiegui and Sorbe, 1999; Sorbe, 1999; Frutos and Sorbe, 2014) against 35-53 in the present study. The reported abundances vary between 114 and 752 ind-100 m^{-2} in several NE Atlantic canyons (Dauvin et al., 1995; Sorbe, 1999; Frutos and Sorbe, 2014) or between 238 and 271 ind.100 m^{-2} in the Bay of Biscay slope (Elizalde et al., 1993; Dauvin et al., 1995), against 4-36 ind.100 m^{-2} in the present study. Our results also show a West-East impoverishment in the number of species and abundance as the main longitudinal trend of the suprabenthos, and suggest a relation between the changes in community structure and surface productivity (relation to surface productivity proxies such as fluorescence, pelagic micro-, meso- and macrozooplankton biomass). This is consistent with previous studies that have repeatedly reported a West-East decrease in abundance and number of species associated to a decrease of productivity and hence in food availability at the seafloor for other deep-sea benthic compartments such as meiofauna (Danovaro et al., 1999), macrofauna (Baldrighi et al., 2014) and megafauna (Tecchio et al., 2011b, 2013). In the western basin, Cartes et al. (2001, 2003) found higher suprabenthic abundances and biomasses in the highly productive Catalan sea (a region influenced by river inputs and the occurrence of submarine canyons), than in the relatively low productivity southern Balearic region (depth range of the studies: 500-1800 m, sampling gear: Macer-Giroq sledge). This example shows that even at the basin scale variations in productivity are considered important drivers for the suprabenthos.

Furthermore, we also found changes in the trophic structure of the assemblages along the longitudinal gradient and an impoverishment in the number of trophic groups and trophic biodiversity in the eastern basin. These results may be interpreted in relation to the extreme oligotrophy reported for the eastern region, where the scarcity of food supply to the seafloor is well documented (Azov, 1986; Psarra et al., 2000). The efficiency of OM transfer to the seafloor at 1000 m depth was estimated as 10% in the western basin vs. 2-3% in the eastern basin (Danovaro et al., 1999; Pusceddu et al., 2010). This longitudinal decrease in OM fluxes to the seafloor may explain the higher relative contribution of groups exploiting food sources in the water column (e.g. predators on zooplankton such as eusirid and hyperiid amphipods) and decreased relative contribution of groups exploiting food sources from the sediment (predators on meiofauna such as oedicerotid amphipods and cumaceans) observed in the eastern basin assemblages.

Within each basin, bathymetric trends in biodiversity and food availability mirrored the observed longitudinal patterns (decrease in abundance, number of species and number of trophic groups) with a marked transition between 1200 and 2000 m. High values of turnover with depth, especially between 1000 and 2000 m, were also reported by Cartes et al. (2003) in the western region. Local settings (e.g. steepness of the slope and distance from mainland; local hydrodynamic conditions, high decomposition rates in the water column (Danovaro et al., 1999)) may further interact with trophic conditions and biodiversity patterns at the region level. For instance, at the basin scale, the bathyal sediments in the western and central regions, are affected by turbidity flows resulting from trawling disturbance (Puig et al., 2012) and periodic cascading events (Canals et al., 2006; Company et al., 2008). These conditions contrast with the more stable hydrologic conditions of the south of Crete (Tselepides et al., 2000).

Interestingly, the changes in the suprabenthic community structure and composition across regions were more pronounced at greater depths while at the shallower sites (1200 m) the assemblages were richer and more similar across regions. In fact, not only food limitation in the East may be particularly aggravated by the increasing depth, but also the physical and oceanographic confinement of the greater depths is increasing eastwards because physical barriers (Strait of Sicily; Strait of Kithyra) may limit species dispersal and bathyal colonization (Bouchet and Taviani, 1992).

Our study did not show a clear trend in diversity indices other than number of species (*H'*, *J'*, $ES_{(n)}$) either with longitude or depth. A comparison of different faunal compartments (Danovaro et al., 2010) also found high variability in diversity in several benthic compartments along the longitudinal gradient without any significant patterns across regions.

2.3.4.2 Vertical distribution and functional traits of suprabenthic species

Similar to previous studies on the suprabenthos from the bathyal Mediterranean Sea (e.g. Madurell and Cartes, 2003; Cartes et al., 2011) and other Atlantic regions (e.g. Cunha et al., 1997; Sorbe, 1999), the assemblages that we studied herein were dominated by peracarids. This faunal component was concentrated in the immediate vicinity of the seafloor with much lower abundances in the upper water layer (50-140 cm). A stratified distribution of peracarids in the near-bottom water column according to their functional traits (e.g. swimming activity, migratory behaviour, feeding habitats and, especially, dependence on water column/epibenthic food sources) was observed. Well-known inhabitants of the Mediterranean suprabenthos such as the dominant mysid *Boreomysis arctica*, the bathypelagic euphausiids *Eupahusia kronii* and *Nematoscelis megalops* (Cartes et al., 1994; Cartes and Sorbe, 1998) and hyperiid amphipods which have high swimming rates and exploit food sources from the water column, occurred throughout the sampled water column, but had a higher relative contribution in the upper layer (50-140 cm). Another common Mediterranean species, the gammaridean amphipod *Rhachotropis caeca* (Cartes and Sorbe, 1999) is an active predator and was also found in both layers. On the other hand, most gammaridean amphipods, cumaceans (e.g. *Campylaspis* spp. and *Procampylaspis armata*) and isopods (e.g. *Munnopsurus atlanticus*) that have lower swimming rates (Dauvin et al., 1995; Cartes and Sorbe, 1997, 1999) and exploit food sources at the sediment surface occurred mostly in the near-bottom layer.

Stable isotope analyses (Fanelli et al., 2009) showed that feeding guilds in the suprabenthos are highly diverse, as these organisms are able to explore a wide range of primary food sources near the seafloor, such as deposited and resuspended POM and small invertebrates. Our results show a relevant contribution of highly mobile taxa with epibenthic food sources (e.g. filter feeders and zooplankton predators) and species with mixed diets that can switch their feeding mode in response to changes in vertical carbon flux (Billet et al., 1983; Cartes et al., 1994), or resuspension phenomena (Lampitt, 1985).

In the near-bottom layer, the studied assemblages showed higher taxonomic and trophic diversity and positive correlations with proxies of organic fluxes to the seafloor (e.g. $ES_{(30)}N1$ with microzooplankton and fluorescence). The putative effects of decreased food availability at the seafloor with increasing depth are markedly deleterious for their abundance and biodiversity, and the extreme oligotrophy of the eastern basin accentuates these bathymetric changes. Besides the overall closer interaction with the sediment, the lower swimming rates and dispersal capabilities of the species typically found in the near-bottom layer are also likely to limit their ability to colonize and maintain large populations in the more confined conditions of the West-East gradient. In this way, they mirror the well-known impoverished benthic assemblages of the deep Mediterranean Sea (Emig and Geistdoerfer, 2004; Coll et al., 2010).

In the upper water layer, the overall changes in abundance and trophic diversity were less marked, while changes in community structure and composition were more dynamic. The relief in the dominance of filter-feeding mysids both eastwards and towards greater depths was accompanied by the occurrence of a richer and more even assemblage of hyperiids and euphausiids (mostly zooplankton predators). Lower dependence on seafloor trophic resources and increased mobility of the species typically found in the upper layer is likely to be advantageous in food limited environments (Tselepides et al., 2000; Baldrighi et al., 2014). It also allows avoidance of unsuitable conditions and increases dispersal capability of adults. Moreover, euphausiids and decapods have further enhanced dispersal capabilities by producing larvae and are probably less affected by the physical and oceanographic confinement.

2.3.5 Conclusions

Since the late 1980s, several quantitative studies using sledges with superimposed nets contributed significantly to the knowledge of suprabenthos in the Mediterranean Sea and elsewhere. Cartes et al. (2001, 2011) showed that the study of the vertical distribution in the water column just above the sediment is of utmost importance to understand distribution patterns of these dynamic assemblages. However, many deep-sea suprabenthic studies have been focused on the total fauna irrespective of the water layer or only on the fauna collected at the near–bottom layer. The fauna from the upper nets have been frequently overlooked due to its typical low abundance and also because there are technical difficulties in sampling efficiently this biological component. Furthermore, the trophic structure of suprabenthic assemblages is not often analysed, and even less so in relation to the near-bottom distribution.

Our results show that the analysis of the near-bottom vertical distribution of the suprabenthos revealed interesting complex trends in community structure (both taxonomic and trophic) and biodiversity (both α- and β-diversity) across all spatial scales. In fact, the small-scale dynamics of this stratified vertical distribution helps understanding the observed large-scale trends (or apparent lack of them).

The deep-sea Mediterranean fauna has been presented from a metacommunity perspective as mostly constituted by an impoverished subset of the NE Atlantic fauna (Bellan-Santini, 1990; Bouchet and Taviani, 1992; Coll et al., 2010). The marked latitudinal and bathymetric resource gradients enhance the importance of environmental sorting (Leibold et al., 2004) and the occurrence of successive physical barriers to dispersal may prevent rescue or source-sink effects, ultimately leading to impoverished assemblages towards the eastern basin. In the suprabenthic assemblages, the variety in life cycles and functional traits, together with the subsequent vertical distribution of the organisms, allow a flexible community structure. Here, the faunal components in the near-bottom and upper water layers are apparently responding differently to various environmental challenges imposed by the longitudinal and bathymetric gradients (as illustrated by asynchronous turnover, changes in abundance, number of species and trophic structure). We suggest that the near-bottom component is likely to be modulated by environmental sorting and limited dispersal while the more mobile component (species occurring in the upper layer or throughout the sampled water column) is still affected by environmental sorting but dispersal mechanisms are more efficient. Curiously, the sum up of the fluctuations in different components appears to result in the maintenance of relatively constant values of diversity indices either across depths or regions. Of course, the typically low densities of the bathyal suprabenthos in the Mediterranean Sea (even more at the upper water layer) and the low number of study sites investigated, impose important limitations to our interpretation which must be considered as a hypothesis to be tested by future investigations.

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Supplementary material

Table S2.3.1. List of the environmental variables used in the environmental analysis for each site.

Figure S2.3.1 Relative abundance (%) of the major taxonomic groups of suprabenthos from the Mediterranean Sea.

Table S2.3.2. 10 dominant taxa of suprabenthos collected with a suprabenthic sledge in the two water layers (N1:0–50 cm and N2+N3: 55-140 cm) at all the sites. W: western basin; C: central basin; E: eastern basin.

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Table S2.3.1 List of the environmental variables used in the environmental analysis for each site. DO: dissolved oxygen; FTU: Formazin turbidity units; POC: particulate organic carbon; micropl. biom.: microzooplankton biomass; mesozoopl.: mesozooplankton biomass; DSL macroplank. biom.: macrozooplankton biomass in the deep scattering layer; RFU: relative flourescence units (proxy for surface primary production); W: western basin (R1 and R2 refer to the two hauls collected at 1200 m), C: central basin, E: eastern basin.

	R1W1200	R2W1200	W2000	W3000	C1200	C2000	C3000	E1200	E2000	E3000
Benthic temperature (°C)	13.07	13.07	13.21	13.32	13.73	13.78	13.95	13.86	13.91	13.92
Benthic salinity	38.47	38.47	38.47	38.47	38.74	38.73	38.73	38.78	38.77	38.74
Benthic DO (mgl.l^{-1})	5.7	5.7	5.82	5.83	5.73	5.83	5.86	5.53	5.6	5.72
Benthic turbidity (FTU)	0.77	0.77	0.035	0.04	0.072	0.059	0.028	0.04	0.037	0.032
Sediment grain size (% coarse)	1.72	1.72	7.64	16.87	1.08	1.19	4.04	10.48	8.61	12.02
Sediment POC (% of mass)	0.42	0.42	0.52	0.33	0.64	0.58	0.28	0.34	0.26	0.29
0-200 m micropl. biom. (mg m^{-3})	5.39	5.39	9.36	5.05	5.25	3.96	3.74	2.28	4.77	3.94
0-200 m mesopl. biom. (mg m^{-3})	4.19	4.19	11.93	8.3	11.85	10.74	7.89	5.25	10.04	6.11
Fluorescence (RFU)	0.739	0.739	0.927	0.803	0.559	0.657	0.745	0.541	0.641	0.667
DSL macroplank. biom. (g.m^{-3})	10.82	10.82	0.80	0.57	0.76	0.51	0.35	0.38	0.48	0.45

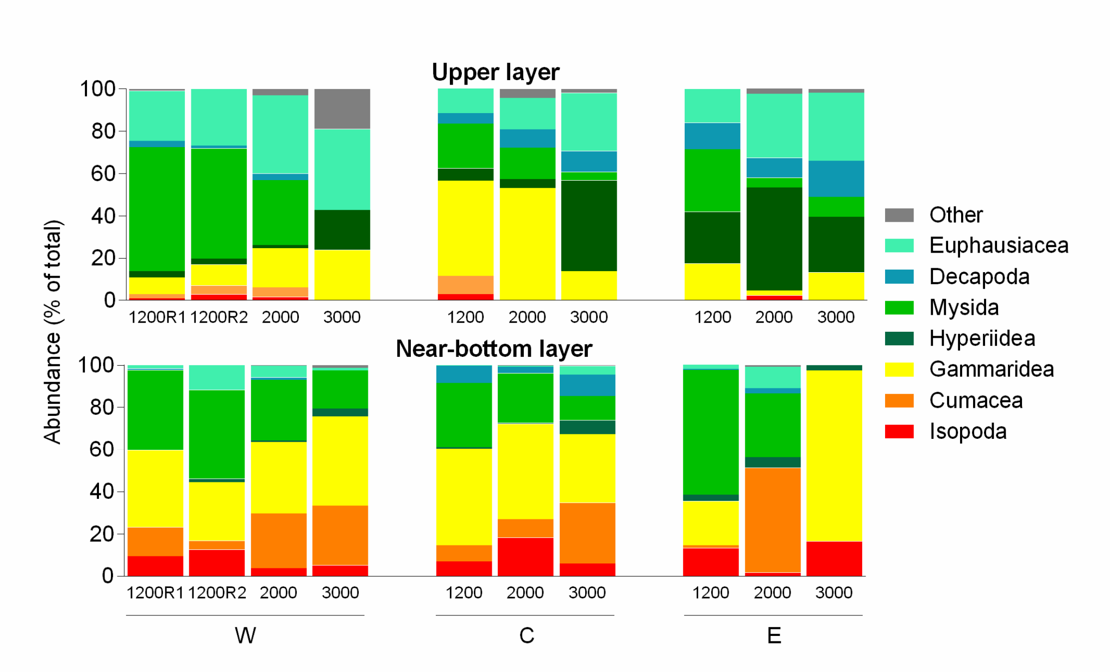

Figure S2.3.1 Relative abundance (%) of the major taxonomic groups of suprabenthos from the Mediterranean Sea. Near-bottom layer (N1: 10-50 cm); upper layer (N2+N3: 55-140 cm); W: western basin; C: central basin; E: eastern basin. Other: Tanaidacea, Lophogastrida and Leptostraca.

Table S2.3.2 10 dominant taxa of suprabenthos collected with a suprabenthic sledge in the two water layers (N1:0–50 cm and N2+N3: 55-140 cm) at all the sites. W: western basin, C: central basin, E: eastern basin.

N1											
W1200			**%**	**C1200**			**%**	**E1200**			**%**
MYS	EP-Om-mic	*Boreomysis arctica*	29.9	MYS	EP-Om-mic	*Boreomysis arctica*	29.1	MYS	EP-Om-mic	*Boreomysis arctica*	28.6
GAM	EP-Pr-zoo	*Rhachotropis caeca*	9	GAM	EP-Pr-zoo	*Rhachotropis caeca*	15.7	MYS	EP-Om-mic	*Parerythrops lobiancoi*	16.6
ISO	SR-Om-mic	*Munnopsurus atlanticus*	6.9	DEC	SR-Om-mac	*Calocaris macandreae*	6.9	GAM	SR-Dt	*Mediterexis mimonectes*	7.5
MYS	EP-Om-mic	Mysida und.	6.1	GAM	EP-Pr-zoo	*Epimeria cornigera*	5	MYS	EP-Om-mic	Mysida und.	7.5
GAM	SS-Pr-mei	*Bathymedon longirostris*	5.3	GAM	SR-Sc-mac	*Lysianassa plumosa*	5	ISO	SR-Om-mic	*Munnopsurus atlanticus*	7.4
GAM	EP-Pr-zoo	*Ileraustroe ilergetes*	4.1	ISO	EP-Sp-fis	*Aegiochus incisa*	4.2	MYS	EP-Om-mic	*Calyptomma puritani*	5
GAM	SR-Dt	*Mediterexis mimonectes*	3.7	GAM	U	Gammaridea und.	3.4	GAM	EP-Pr-zoo	*Rhachotropis caeca*	4.7
GAM	EP-Pr-zoo	*Rhachotropis* und	2.6	GAM	EP-Pr-zoo	*Rhachotropis rostrata*	2.7	ISO	SR-Om-mic	Eurycopinae und.	2.8
CUM	SS-Pr-mei	*Campylaspis* cf. *glabra*	2.6	GAM	SR-Sc-mac	*Tryphosa nana*	2.3	GAM	EP-Pr-zoo	*Epimeria cornigera*	1.8
CUM	SR-Gr-mic	*Platysympus typicus*	2.4	GAM	SR-Sc-mac	*Tmetonyx similis*	2.3	HYP	EP-Pr-zoo	*Anchylomera blossevillei*	1.3
Total			72.6	Total			76.6	Total			83.3
W2000			**%**	**C2000**			**%**	**E2000**			**%**
MYS	EP-Om-mic	*Boreomysis arctica*	20.5	GAM	EP-Pr-zoo	*Rhachotropis caeca*	27	CUM	SR-Gr-mic	*Platysympus typicus*	26.1
GAM	EP-Pr-zoo	*Rhachotropis caeca*	11.4	MYS	EP-Om-mic	*Boreomysis arctica*	13.5	MYS	EP-Om-mic	*Boreomysis arctica*	18.5
CUM	SS-Pr-mei	*Procampylaspis armata*	7.3	ISO	SR-Om-mic	*Munnopsurus atlanticus*	9.6	CUM	SR-Gr-mic	*Vaunthompsonia caeca*	15.1
CUM	SR-Gr-mic	*Platysympus typicus*	6.8	MYS	EP-Om-mic	Mysida und.	5.5	MYS	EP-Om-mic	Mysida und.	8.4
MYS	EP-Om-mic	Mysida und.	6	ISO	SR-Om-mic	*Disconectes* cf. *phalangium*	4.4	CUM	SS-Pr-mei	*Procampylaspis armata*	4.2
EUP	EP-Pr-zoo	*Nematoscelis megalops*	5.5	CUM	SS-Pr-mei	*Campylaspi*s spp.	4.1	EUP	EP-Om-mic	*Euphausia hemigibba*	4.2
GAM	EP-Pr-zoo	*Bruzelia typica*	4.7	GAM	EP-Pr-zoo	*Rhachotropis rostrata*	3.3	EUP	EP-Om-mic	Euphausiidae und.	4.2
GAM	EP-Pr-zoo	*Pseudotiron bouvieri*	4.7	ISO	SR-Om-mic	*Ilyarachna longicornis*	3.3	MYS	EP-Om-mic	*Paramblyops rostratus*	3.4
GAM	SR-Dt	*Mediterexis mimonectes*	3.4	GAM	U	Gammaridea und.	2.8	DEC	SR-Om-mac	*Gennadas elegans*	2.5
CUM	SS-Pr-mei	*Campylaspis horridoides*	3.4	MYS	EP-Om-mic	*Paramblyops rostratus*	2.5	HYP	EP-Pr-zoo	Hyperidea und.	1.7
Total			73.5	Total			76	Total			88.2

W3000			%	**C3000**			%	**E3000**			%
CUM	SS-Pr-mei	*Campylaspis* cf. *glabra*	12.8	CUM	SR-Gr-mic	*Platysympus typicus*	22.1	GAM	EP-Pr-zoo	*Rhachotropis caeca*	59.9
MYS	EP-Om-mic	*Boreomysis arctica*	10.3	GAM	EP-Pr-zoo	*Rhachotropis caeca*	12.1	ISO	SR-Om-mic	*Munnopsurus atlanticus*	14.5
GAM	EP-Pr-zoo	*Epimeria cornigera*	7.7	MYS	EP-Om-mic	*Boreomysis arctica*	9.5	GAM	EP-Pr-zoo	*Pseudotiron bouvieri*	5.3
GAM	SR-Sc-mac	*Tryphosa nana*	7.7	GAM	EP-Pr-zoo	*Pseudotiron bouveri*	8.5	GAM	EP-Pr-zoo	*Bruzelia typica*	4.6
MYS	EP-Om-mic	Mysida und.	7.7	ISO	SR-Om-mic	*Munnopsurus atlanticus*	5.5	GAM	SR-Dt	*Mediterexis mimonectes*	3.3
GAM	SR-Sc-mac	*Tmetonyx* cf. *dilatata*	6.4	DEC	EP-Pr-zoo	*Nematocarcinus exilis*	4.5	GAM	EP-Pr-zoo	*Epimeria cornigera*	2
GAM	EP-Pr-zoo	*Bruzelia typica*	5.1	GAM	EP-Pr-zoo	Rhachotropis und.	4	GAM	SR-Om-mac	*Scopelocheirus hopei*	2
GAM	EP-Pr-zoo	*Pseudotiron bouveri*	5.1	GAM	U	Gammaridea und.	3.5	GAM	EP-Pr-zoo	*Ileraustroe ilergetes*	2
HYP	EP-Pr-zoo	*Hyperia* spp.	3.8	CUM	SR-Gr-mic	*Vamthompsonia caeca*	2.5	HYP	EP-Pr-zoo	*Themisto* sp.	1.3
GAM	U	Gammaridea und.	3.8	CUM	SS-Pr-mei	*Campylaspis* cf. *glabra*	2.5	ISO	SR-Om-mic	*Ilyarachna longicornis*	1.3
Total			70.5	Total			74.9	Total			96.1

N2+N3

W1200			%	**C1200**			%	**E1200**			%
MYS	EP-Om-mic	*Boreomysis arctica*	53.2	MYS	EP-Om-mic	*Boreomysis arctica*	17.3	MYS	EP-Om-mic	*Boreomysis arctica*	22.2
EUP	EP-Om-mic	*Euphausia krohnii*	15.6	GAM	EP-Pr-zoo	*Rhachotropis caeca*	15.4	HYP	EP-Pr-zoo	*Primno macropa*	8.6
EUP	EP-Pr-zoo	*Nematoscelis megalops*	8.1	GAM	EP-Pr-zoo	*Epimeria cornigera*	3.8	GAM	EP-Pr-zoo	*Rhachotropis rostrata*	8.6
GAM	EP-Pr-zoo	*Rhachotropis caeca*	2.3	GAM	SR-Sc-mac	*Lysianassa plumosa*	3.8	DEC	SR-Pr-mac	*Acanthephyra eximia*	8.6
CUM	SR-Gr-mic	*Platysympus typicus*	2.3	GAM	EP-Pr-zoo	*Bruzelia typica*	3.8	EUP	EP-Om-mic	*Euphausia hemigibba*	6.2
MYS	EP-Om-mic	Mysida und.	2.3	MYS	EP-Om-mic	Mysida und.	3.8	HYP	EP-Pr-zoo	*Hyperioides longipes*	4.9
DEC	SR-Om-mac	*Gennadas elegans*	1.7	EUP	EP-Om-mic	*Euphausia krohnii*	3.8	MYS	EP-Om-mic	Mysida und.	4.9
GAM	SR-Sc-mac	*Tryphosella* cf. *nanoides*	1.2	HYP	EP-Pr-zoo	*Vibilia armata*	2.9	GAM	EP-Pr-zoo	*Epimeria cornigera*	3.7
GAM	SS-Pr-mei	Oedicerotidae und.	1.2	GAM	EP-Pr-zoo	*Syrrhoites pusilla*	2.9	GAM	EP-Om-mic	*Stylocheiron longicorne*	3.7
GAM	EP-Pr-zoo	*Pseudotiron bouvieri*	1.2	GAM	U	Gammaridea und.	2.9	EUP	EP-Om-mic	Euphausiidae und.	3.7
Total			89	Total			60.6	Total			75.3

W2000			%	**C2000**			%	**E2000**			%
EUP	EP-Pr-zoo	*Nematoscelis megalops*	27.3	GAM	EP-Pr-zoo	*Rhachotropis caeca*	21.3	HYP	EP-Pr-zoo	*Primno macropa*	18.6
MYS	EP-Om-mic	*Boreomysis arctica*	21.2	GAM	SR-Om-mac	*Scopelocheirus hopei*	21.3	EUP	EP-Om-mic	*Euphausia hemigibba*	18.6
MYS	EP-Om-mic	Mysida und.	9.1	MYS	EP-Om-mic	*Boreomysis arctica*	14.9	HYP	EP-Pr-zoo	*Hyperioides* sp.	14
GAM	EP-Pr-zoo	*Rhachotropis caeca*	4.5	EUP	EP-Pr-zoo	*Nematoscelis megalops*	10.6	HYP	EP-Pr-zoo	Hyperiidae juv.	9.3
GAM	EP-Pr-zoo	*Pseudotiron bouvieri*	4.5	GAM	EP-Pr-zoo	*Rhachotropis rostrata*	4.3	DEC	SR-Om-mac	*Gennadas elegans*	9.3
CUM	SS-Pr-mei	Nannastacidae und.	4.5	GAM	U	Gammaridea und.	4.3	EUP	EP-Om-mic	*Euphausia krohnii*	7
EUP	EP-Om-mic	*Euphausia krohnii*	4.5	LOPH	EP-Pr-zoo	*Eucopia unguiculata*	4.3	MYS	EP-Om-mic	*Boreomysis arctica*	4.7
EUP	EP-Om-mic	*Stylocheiron longicorne*	4.5	DEC	SR-Om-mac	*Gennadas elegans*	4.3	HYP	EP-Pr-zoo	*Themisto* sp.	2.3
GAM	EP-Pr-zoo	*Rhachotropis* und.	3	HYP	EP-Pr-zoo	*Hyperioides* sp	2.1	HYP	EP-Pr-zoo	*Hyperia* spp.	2.3
GAM	U	Gammaridea und.	3	HYP	EP-Pr-zoo	*Phrosina semilunata*	2.1	HYP	EP-Pr-zoo	*Rhabdosoma brevicaudatum*	2.3
Total			86.4	Total			89.4	Total			88.4
W3000			%	**C3000**			%	**E3000**			%
GAM	U	Gammaridea und.	19	HYP	EP-Pr-zoo	*Hyperioides* sp.	11.8	EUP	EP-Om-mic	*Euphausia hemigibba*	20.8
LOPH	EP-Pr-zoo	*Eucopia unguiculata*	19	HYP	EP-Pr-zoo	*Hyperia* spp.	9.8	GAM	EP-Pr-zoo	*Rhachotropis caeca*	11.3
HYP	EP-Pr-zoo	Hyperiidae juv.	14.3	EUP	EP-Pr-zoo	*Nematoscelis megalops*	9.8	DEC	SR-Om-mac	*Aristeus antennatus*	9.4
EUP	EP-Om-mic	*Euphausia krohnii*	14.3	HYP	EP-Pr-zoo	*Primno macropa*	7.8	HYP	EP-Pr-zoo	*Hyperioides longipes*	7.5
EUP	EP-Om-mic	Euphausiidae und.	14.3	GAM	U	Gammaridea und.	7.8	MYS	EP-Om-mic	Mysida und.	7.5
EUP	EP-Pr-zoo	*Nematoscelis megalops*	9.5	DEC	U	Decapoda und.	5.9	DEC	U	Decapoda und.	5.7
HYP	EP-Pr-zoo	*Primno macropa*	4.8	EUP	EP-Om-mic	*Euphausia krohnii*	5.9	HYP	EP-Pr-zoo	*Primno macropa*	3.8
HYP	EP-Pr-zoo	*Scopelocheirus hopei*	4.8	HYP	EP-Pr-zoo	Hyperiidae juv.	3.9	HYP	EP-Pr-zoo	*Phrosina semilunata*	3.8
				MYS	EP-Om-mic	Mysida und.	3.9	EUP	EP-Om-mic	*Meganyctiphanes norvegica*	3.8
				EUP	EP-Om-mic	*Meganyctiphanes norvegica*	3.9	HYP	EP-Pr-zoo	*Themisto* sp.	1.9
Total			100	Total			70.6	Total			75.5

Taxonomic groups (GAM: gammaridean amphipod; HYP: hyperid amphipod; ISO: isopod; CUM: cumacean; DEC: decapod; EUP: euphausiid). Functional groups (EP: water column, SR: surface, SS: subsurface; sed: sediment, mic: microfauna, mei: meiofauna, mac: macrofauna, zoo: zooplankton, Dt: detritus feeder, Su: suspension/filter feeder, Pr: predator, Sc: scavenger, Gr: grazer, Om: omnivorous). Und.: undetermined or damage specimens; juv. juvenile specimens. Note: W1200, weighted average of W1200R1 and W1200R2.

2.4 Biodiversity of suprabenthic peracarid assemblages from the Blanes Canyon region (NW Mediterranean Sea) in relation to natural disturbance and trawling pressure

Almeida, M., Frutos, I., Company, J.B., Martin, D., Cunha, M.R. (published online 2016). Biodiversity of suprabenthic peracarid assemblages from the Blanes Canyon region (NW Mediterranean Sea) in relation to natural disturbance and trawling pressure. Deep-Sea Research II.

Abstract

Blanes Canyon and its adjacent margin are important fishery areas (mainly by bottom trawling) located in a highly energetic oceanographic setting in the NW Mediterranean Sea. Here we assess the spatial and temporal variability in abundance, diversity and community structure of the suprabenthic peracarid assemblages in this region and examine this variability in relation to the natural and anthropogenic (trawling fisheries) disturbance regimes. The sampling was conducted between March 2003 and May 2004 in three main fishing grounds, the canyon head (average depth: 490 m), the canyon wall (average depth: 550 m) and the eastern adjacent slope (average depth: 820 m), as well as in two non-exploited areas in the western (at 900 m depth) and eastern (at 1500 m depth) slope near the canyon mouth. A total of 138 species were identified, with amphipods being the most speciose and abundant group, followed by mysids in terms of abundance. Our results show high spatial and temporal variability in suprabenthic assemblages. Densities were higher in the canyon head and western slope, which appear to be the preferential routes for water masses and particle fluxes in months of flood events, and other energetic processes. In the canyon head, where periodic erosion processes are more active, low diversity, high dominance and higher turnover (β-diversity) were observed, apparently coupled with significant temporal fluctuations in the densities of the highly motile component of suprabenthos (mysids, predatory and scavenging amphipods). In the sedimentary more stable eastern slope, high diversity values were observed, accompanied by a higher relative contribution of the less motile groups (i.e. amphipods, most isopods, cumaceans). These groups have a closer interaction with the sediment where they exploit different food sources and are more susceptible to physical disturbance. Temporal variability in their diversity may be related to changes in food quality rather than quantity. In the canyon wall, temporal fluctuations in diversity indices were only revealed in relation to the overall higher and more continued fishing pressure observed in the canyon wall fishing ground (Cara Norte/Sot site). Here, species richness and abundance declined with increasing fishing pressure but the lowest trophic and taxonomic diversities were observed under intermediate levels of disturbance. These findings underline i) the differences between relatively low and highly motile taxa in terms of response to disturbance events; ii) the differences between assemblages subjected to different levels of natural disturbance and trawling pressure, which modify the common bathymetric patterns of abundance and diversity often described from continental margins.

2.4.1 Introduction

Submarine canyons are steep-walled valleys that incise continental margins, where they create unusual high variation in abundance and diversity of biological communities by increasing heterogeneity as well as affecting disturbance and productivity regimes (Levin et al., 2001; Cunha et al., 2011; Harris and Whiteway, 2011). Submarine canyons are the primary conduits of particulate material to the deep basin. Their topography affects local oceanography at different temporal scales (e.g. diverse current regimes, turbidity flows, cascading, re-suspension of particle flow) (Canals et al., 2006, 2013; Sanchez-Vidal et al., 2008; Zúñiga et al., 2009; López-Fernández et al., 2013), favors the occurrence of localized areas of organic enrichment (Vetter and Dayton, 1999; López-Fernández et al., 2013) and provides varied physical habitats (e.g. steep slopes, sedimentary terraces, rock outcrops and diverse substrate types) (Hargrave et al., 2004; Schlacher et al., 2007), thus creating different levels of heterogeneity and disturbance (Harris, 2014). Canyons are also subjected to anthropogenic influences, such as litter accumulation (Ramírez-Llodrà et al., 2013), chemical pollution (Sanchez-Vidal et al., 2015) and fisheries (Company et al., 2012; Pusceddu et al., 2014), which cause additional disturbance and play an important role in the dynamics of the canyon systems.

The complexity of canyon systems may benefit the benthic fauna in several ways, allowing the occurrence of a high functional diversity from sessile to highly motile species, suspension feeders, detritivores and deposit feeders, planktivores and scavengers (Shepard et al., 1974; Macquart-Moulin and Patriti, 1996, Vetter and Dayton, 1999, Vetter et al., 2010). Because they concentrate sediments rich in phytodetritus and other sources of organic matter, canyons show frequently enhanced abundances and/or biomasses of benthic and pelagic fauna (e.g. Albaina and Irigoien, 2007; McClain and Barry, 2010; Cunha et al., 2011), but opposite trends may also be found in relation to frequent disturbance events (García et al., 2007; Romano et al., 2013). Diversity patterns in canyons are by no means universal (Schlacher et al., 2007; Cunha et al., 2011; Ingels et al., 2013). Some canyons show high mega-epibenthic diversity (Ramírez-Llodrà et al., 2009; Vetter et al., 2010), but macro- and meiofauna often show high dominance of a few species and therefore diversity indices are frequently reduced in relation to the adjacent open slope at equivalent depths (Gage et al., 1995; Bianchelli et al., 2010). Canyon size, depth, complexity of configuration, local oceanography and anthropogenic impact, among other factors, influence these patterns (e.g. Schlacher et al., 2007; Ramírez-Llodrà et al., 2009; Cunha et al., 2011) and therefore, canyon systems contribute significantly to regional diversity (Cunha et al., 2011) and fisheries productivity (Company et al., 2008).

Canyon topography generally provides nursery and spawning areas for megafaunal species including those of commercial value (Sardà et al., 1994, 2009; Stefanescu et al., 1994; Sardà and Cartes, 1997). By their proximity to the mainland, shelf-incising canyons are especially targeted for fisheries and their benthic assemblages are often exposed to bottom trawling (Harris and Whiteway, 2011). Recent evidence of trawling impacts on slopes and submarine canyons includes changes in sediment properties (e.g. reduction in organic carbon, erosion and mixing sediments), seafloor morphology (smother topography), increased water turbidity (Puig et al., 2012; Martín et al., 2014) as well as changes in the structure of benthic assemblages (e.g. by removal of large predators and sessile epifauna) (Ramírez-Llodrà et al., 2009; Miller et al., 2012, Pusceddu et al., 2014). These impacts can affect larger areas than the ones directly affected (e.g. by extended sediment plumes) (Puig et al., 2012; Martín et al., 2014). Some alterations in the biodiversity and community structure of benthic assemblages are the elimination of rare and/or sensitive species, the increased dominance of scavengers and a few tolerant/opportunistic species, as well as the reduction of the mean body size of dominant species (Gage et al., 2005).

The knowledge on the dynamics of biological assemblages subjected to disturbance is fundamental to understand the relationships between the structure and functioning of the ecosystems and the natural and anthropogenic environmental factors that affect them. Here, we address suprabenthic assemblages, a key compartment of deep-sea food webs composed by small-sized fauna (mainly peracarid crustaceans), with varied feeding modes and life styles (Madurell et al., 2008; Fanelli et al., 2009), that establish a strong relationship with the seafloor but are also characterized by their diel vertical migrations (Brunel et al., 1978). Together with other fauna in the deep scattering layer, suprabenthos has an important role in recycling organic matter towards the pelagic ecosystem (Dilling and Aldrege 2000; Trueman et al., 2014).

Suprabenthic assemblages are a major food resource for benthic and bentho-pelagic fish, epibenthic crustaceans and cephalopods, many of which with commercial value (Carrassón and Cartes, 2002, Fanelli et al., 2009). In this region, suprabenthos is part of the diet of the deep-sea rose shrimp *Aristeus antennatus* (Risso, 1816), which has been regularly targeted by crustacean trawlers for the past seven decades at depths from 300 to 900 m depth (Sardà and Cartes, 1997; Sardà et al., 2009; Gorelli et al., 2014). Under the scope of the RECS II project (Integral Study of a Submarine Canyon in the Western Mediterranean Sea (Blanes Canyon): Application to the exploitation of the deep-water rose shrimp), a multidisciplinary study was undertaken to characterise the hydrodynamic conditions and benthic assemblages in the Blanes Canyon region and their relationships to the rose shrimp fisheries (Ramírez-Llodrà et al., 2009, Sardà et al., 2009; Zúñiga et al., 2009; Romano et al., 2013). Here we aim at 1) describing the spatial and temporal variability of the suprabenthic assemblages in the Blanes Canyon region and 2) examining this variability in relation to natural and anthropogenic disturbance regimes (e.g. current flow, particle fluxes and shrimp trawling fisheries).

2.4.2 Material and methods

2.4.2.1 Study area

Blanes Canyon is the largest canyon in the Catalan margin, NW Mediterranean (Fig. 2.4.1). Here, the circulation is dominated by the North Current (NC) which is mainly forced by the Atlantic Water (AW) incoming through the Gibraltar Strait and extending from the surface down to 100–200 m depth. The more saline Levantine Intermediate Water (LIW), originating in the eastern Mediterranean basin, extends down to approximately 600 m depth and the Western Mediterranean Deep Water (WMDW), which forms during the winter in the Gulf of Lion, extends down to the seafloor (Millot, 1999). Wind-induced cooling and evaporation of surface waters during winter in the NW Mediterranean leads to a massive open ocean dense water formation. Coastal surface waters also become denser and these cold and turbid water masses cascade downslope, mainly through submarine canyons. Exceptionally intense cascading events, reaching current speeds >85 cm s^{-1} inside submarine canyons and with high potential dragging capacity, occur at a decadal timescale under very dry, windy and cold winters (Canals et al., 2006).

The Blanes Canyon head incises the continental shelf at 60 m depth, less than 4 km offshore, in a NW-SE direction (Lastras et al., 2011). The width increases with depth and reaches a maximum of 20 km wide when the canyon meets the Valencia Channel at 2400 m deep. The upper course of the canyon is characterised by a V-shaped cross-section, indicative of intense erosion processes, and is flanked by several gullies; the lower course has a U-shaped cross-section, indicative of high sediment deposition (Lastras et al., 2011).

The regime of particle fluxes in Blanes Canyon is subjected to a very high spatial and temporal variability determined by its physiography, as well as by the proximity to the Tordera River mouth and weather-driven energetic events, among other inputs of allochtonous and autochtonous materials (Canals et al., 2013; López-Fernández et al., 2013). Sediment resuspension caused by bottom trawling is an additional but relevant source of particle fluxes in the canyon region (Puig et al., 2012; López-Fernández et al., 2013; Martín et al., 2014).

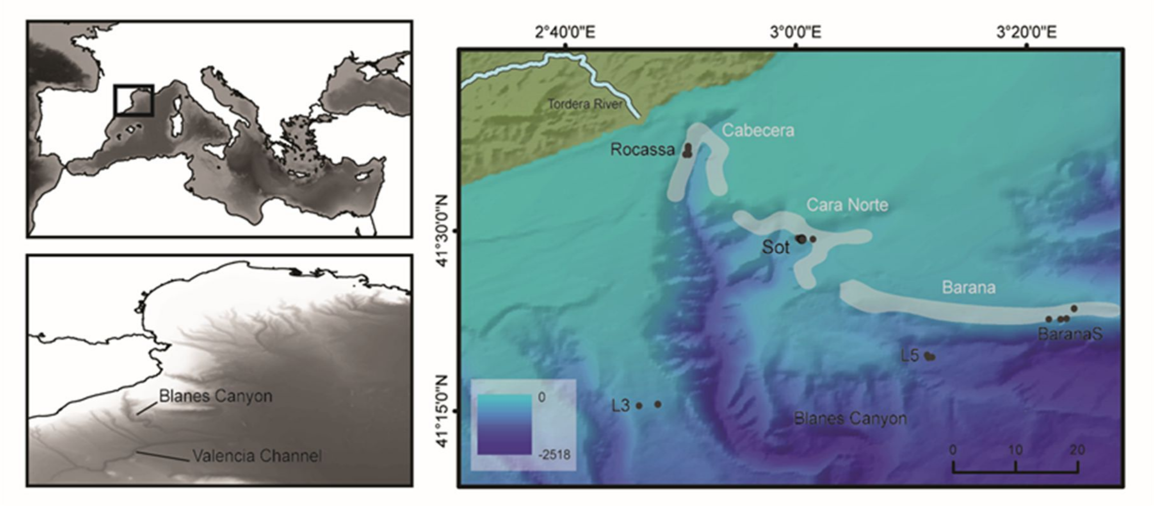

Figure 2.4.1 Location of the study sites (dots) and the three main fishing grounds (shaded areas) in the Blanes canyon region, Western Mediterranean Sea.

The rose shrimp *A. antennatus* is a resource regularly exploited exclusively by bottom trawling in fishing grounds of the Blanes Canyon region throughout the year. Populations of *A. antennatus* occur mostly in association with relatively salty waters (LIW) and low intensity currents with moderate variability (Sardà et al., 2009). Fluctuations in landings are related to seasonal shifts of the rose shrimp populations in the canyon region, over the shelf and slope. In spring and early summer, catches are mainly composed of mature females and occur on the mid-slope between 600 m and 800 m depth (the Barana fishing ground extending over approximately 162 km^2 of the seafloor; Fig. 2.4.1); in summer the peak of catches occurs in the canyon walls from 500 to 600 m depth (the Cara Norte fishing ground, approx. 99 km^2, Fig. 2.4.1); in autumn and winter, densities in both areas decrease and catches of juveniles, much less abundant, occur at shallower depths in the submarine canyon head (the Cabecera fishing ground, approx. 81 km^2, Fig. 2.4.1) (Sardà et al., 2004, 2009; Gorelli et al., 2014).

2.4.2.2 Sampling

Under the scope of the RECS II project, the relationships of oceanographic processes and benthic assemblages with the spatial-temporal fluctuations of the rose shrimp were investigated over an annual cycle (March 2003 – May 2004) in Blanes Canyon and the adjacent slope. The research strategy included the simultaneous acquisition of hydrographic data (temperature and transmissivity profiles, near-bottom current intensities), organic matter fluxes and sampling of benthic assemblages (mega-epibenthos, suprabenthic macrofauna, endobenthic meiofauna) in fished and non-fished areas. River daily discharges were obtained from official entities and data on the rose shrimp fisheries were obtained from the official fishermen's association of the Blanes harbour and from the logbooks of shrimp trawlers. Details on the methodology and results obtained can be found in Zúñiga et al. (2009) for environmental data, Ramírez-Llodrà et al. (2009) for mega-epifauna, Ingels et al. (2013) and Romano et al. (2013) for meiofauna and Sardà et al. (2009) for population dynamics of *A. antennatus*.

The sampling was conducted during 4 cruises in March, July and November 2003 and May 2004 in the three main fishing grounds, Cabecera in the canyon head (site Rocassa, with an average depth of 490 m), Cara Norte in the canyon wall (site Sot with an average depth of 550 m) and Barana in the eastern adjacent slope (site BaranaS, with an average depth of 820 m), as well as in two non-fished areas in the western (site L3, 900 m depth) and eastern (site L5, 1500 m depth) slope nearby the canyon mouth (Fig. 2.4.1, Table 2.4.1). The positions of L3 and L5 were constrained mainly by the optimisation of environmental data acquisition (location of moorings for sediment traps and currentmeters).

Suprabenthos was collected with a modified version of the Macer-GIROQ sledge (see Cartes et al., 1994 for a full description). This gear is composed with three superimposed nets (0.5 mm mesh size; opening of the net: 80 cm width and 40 cm height) that allow sampling the motile fauna in three water layers above the bottom (10-50, 55-95 and 100-140 cm). The sledge was towed over the seabed around 30-60 min at approximately 1.5 to 2 knots (Table 2.4.1). The collected fauna was sieved through a 0.5 mm mesh and fixed on board with 10% formalin. In the lab, the samples were sorted to major taxa under a dissecting microscope and kept in 70% ethanol.

Table 2.4.1 Metadata of the suprabenthic samples taken from the Blanes canyon region. C: canyon; ES: eastern slope; WS: western slope.

Sample code	Site		Date (d/m/y)	Hour[a] (h:m)	Depth[a] (m)	Coordinates[a] Lat (N)	Lon (E)	Dist.[b] (m)	Area[c] (m^2)
RECS1P4	Rocassa	C	31/03/2003	03:37	466	41° 36' 59"	02º 50' 39"	2413.8	1931.1
RECS3P4	Rocassa	C	09/07/2003	22:38	500	41º 36' 46"	02º 50' 40"	1389.0	1111.2
RECS5P2	Rocassa	C	02/11/2003	00:23	487	41º 36' 21"	02º 50' 27"	972.3	777.8
RECS7P5	Rocassa	C	11/05/2004	06:45	510	41° 36' 20"	02° 50' 42"	1728.5	1382.8
RECS1P3	Sot	C	31/03/2003	00:40	540	41° 29' 18"	03° 01' 29"	2592.8	2074.2
RECS3P3	Sot	C	09/07/2003	19:24	557	41° 29' 22"	03° 00' 12"	2083.5	1666.8
RECS5P1	Sot	C	01/11/2003	17:41	554	41° 29' 17"	03° 00' 30"	1404.4	1123.5
RECS7P4	Sot	C	11/05/2004	04:23	560	41° 29' 16"	03° 00' 34"	1913.8	1531.0
RECS1P1	BaranaS	ES	29/03/2003	21:23	711	41° 23' 43"	03° 25' 27"	1435.3	1148.2
RECS3P2	BaranaS	ES	09/07/2003	13:38	812	41° 22" 40"	03° 23' 28"	1666.8	1333.4
RECS5P3	BaranaS	ES	02/11/2003	12:48	781	41° 22' 37"	03° 21' 56"	2106.7	1685.3
RECS7P2	BaranaS	ES	10/05/2004	00:55	800	41° 22' 36"	03° 22' 57"	1890.6	1512.4
RECS5P6	L3	WS	06/11/2003	11:50	910	41° 15' 33"	02° 48' 02"	1674.5	1339.6
RECS7P3	L3	WS	11/05/2004	00:52	900	41° 15' 26"	02° 46' 25"	2052.6	1642.1
RECS1P2	L5	ES	30/03/2003	03:50	1500	41° 01' 59"	02° 32' 20"	3704.0	2963.2
RECS5P5	L5	ES	06/11/2003	06:45	1517	41° 19' 27"	03° 11' 47"	2916.9	2333.5
RECS7P1	L5	ES	10/05/2004	23:13	1510	41° 19' 26"	03° 11' 30"	2538.8	2031.0

a)at the beginning of the haul; b)estimated seafloor distance sampled by the sledge during the haul; c)estimated seafloor area sampled during the haul.

2.4.2.3 Data analysis

In this study, only the peracarids were accounted for; the remaining fauna in the suprabenthos (copepods, ostracods, euphausiids, decapods and infauna) was not considered. The specimens were identified to species level, whenever possible, and counted. The abundances were expressed as number of individuals per 100 m^2 integrating catches over the 10-140 cm water layer. The swept area (A) was calculated through the following formula: A= SxBTxWx1852 (S: mean speed in knots; BT: time at the seafloor in decimal hours; W: width of the net opening; 1852 is the conversion factor from nautical miles to meters; SxBT corresponds to the estimate of the distance travelled during seafloor sampling).

A trophic guild was allocated to each taxa (adapted from Macdonald et al. (2010) with further information compiled from Madurell et al. (2008) and Fanelli et al. (2009)) using a combination of the following: food source (EP: from the water column; SR: sediment surface; SS: sediment subsurface); diet type (Ca: carnivorous; He: herbivorous; Om: omnivorous); food type/size (sed: sediment; pom: particulate organic matter; mic: microfauna; mei: meiofauna; mac: macrofauna; phy: phytodetritus; zoo:

zooplankton) and feeding mode (De: Deposit feeder, ingests sediment; Dt: Detritus feeder, ingests food particles; Su: Suspension/Filter feeder, Pr: Predator, Sc: Scavenger, Sp: Suctorial parasite, Gr: Grazer, Br: Browser).

The abundance data (total number of specimens) were used to calculate taxonomic and trophic diversity: number of species (S) / trophic groups (TG), Shannon-Wiener diversity index, H' (Shannon and Weaver, 1949), Pielou evenness index, J' (Pielou, 1969) and Hurlbert's expected number of species / trophic groups, $ES_{(n)}$ / $ETG_{(n)}$ (Hurlbert, 1971) for each sample. For S, $ES_{(100)}$, TG and $ETG_{(100)}$ at each site, diversity was partitioned into its α and β components. β-diversity for each site was estimated as $\beta=\gamma-\alpha$ where α is the average diversity at the sample level and γ is the total diversity at the site level (Wagner et al., 2000; Magurran, 2004).

A non-parametric Kruskal-Wallis test (Kruskal and Wallis, 1952) was used to assess the statistical significance of spatial and temporal fluctuations in the abundances of major groups (note: these tests were only performed using the three sites that were sampled in all four sampling occasions: Rocassa, Sot and BaranaS).

For the multivariate analyses of the whole dataset, the density data (ind.100 m^{-2}) were first organized in a species vs. sample matrix. A non-metric multidimensional scaling (nMDS) ordination was performed on square root transformed data using the Bray–Curtis similarity. An analysis of similarities by randomization/permutation tests (ANOSIM) was performed to assess for temporal (sampling occasion), spatial (putatively related to water masses; <600 m, LIW vs. >600 m, WMDW) and fishing-related (fished vs. non-fished areas) differences in the suprabenthic assemblages. A subset of the data including only Rocassa, Sot and BaranaS (representing the three fishing grounds) was analysed in more detail to investigate for spatial and temporal differences in the assemblages and their putative relation to the fishing activity regime. SIMPER analysis (Similarity Percentages – species contributions) was performed to assess the percentage contributions of each species to the similarity within and dissimilarity between the groups. PRIMER v6 software (Clarke and Gorley, 2006) was used for biodiversity and multivariate analyses. The species were also ranked by decreasing abundance to illustrate spatial and temporal changes in dominance.

Commercial capture statistics consisted of daily landing records of the rose shrimp, based on bills of sale on wharf at Blanes harbour. The logbooks used were from eight out of the 13 fishing vessels operating in the region, which corresponded to 80% of the total annual shrimp capture from January 2002 to July 2004. These books provided information on trawling operations in Cabecera, Cara Norte and Barana and included daily biomass landings (kg), tow duration (in hours) and trawling depth. Tow duration was used as a proxy to the fishing effort, expressed as $h.mo^{-1}$, while the biomass landed per km^2 and the trawling time per km^2 were used as estimates of the fishing pressure.

Fishing pressure at each fishing ground was calculated using the monthly accumulated biomass removed (kg of shrimp) and trawling time (h). For comparative purposes, these values were divided by the area of each fishing ground and expressed as $kg.km^{-2}$ and $h.km^{-2}$, respectively. Capture per unit effort (CPUE) was expressed as the biomass removed by one hour of trawling ($kg.h^{-1}$). Density and diversity indices of the suprabenthos were plotted against the average monthly values of fishing pressure ($kg.km^{-2}$) in the 3-month period before each sampling occasion.

2.4.3 Results

2.4.3.1 Environmental data

The environmental data used herein was obtained from previous publications of RECS project (Zúniga et al., 2009; Romano et al., 2013). Over the 1-year period from March 2003 to May 2004, the highest particle fluxes were recorded at the upper canyon (time weighted-fluxes, TWF: up to 14.50 $g.m^{-2}.d^{-1}$ at 600 m depth) where continental inputs associated with the Tordera River are most relevant (Zúniga et al., 2009). The dynamics of water masses and currents through the sharp western flank favoured comparatively high downwards particle fluxes (TWF: 5.95 $g.m^{-2}.d^{-1}$ at 900 m), in contrast to the more stable conditions in the eastern flank (TWF: 1.95 $g.m^{-2}.d^{-1}$ at 900 m) also reflected by its smoother slope (Zúniga et al., 2009). In the adjacent slope, particle fluxes were several orders of magnitude lower than at similar depths in the canyon axis and flanks (TWF at the slope, 1500 m: $5.42x10^{-3}$ $g.m^{-2}.d^{-1}$; at the canyon axis, 1700 m: 4.35 $g.m^{-2}.d^{-1}$; Zúniga et al., 2009). Temporal variations in particle fluxes were determined by increases in river discharges during autumn and winter, with peaks in October and December 2003, and March 2004 (78, 53 and 97 $m^3.s^{-1}$, respectively) and moderate dense shelf water cascading in winter (Zúniga et al., 2009). Although with average speeds usually below 5.5 $cm.s^{-1}$, near-bottom currents attained rather frequently values greater than 15 $cm.s^{-1}$ at the upper canyon (and, to a lesser extent, also on the western flank) during winter and early spring. Such intensities were less frequent towards greater depths and at the eastern flank, and rarely occurred during the summer period (Zúniga et al., 2009; Romano et al., 2013).

The high influence of the continental input is reflected by the dominance of lithogenic refractory material and a significant fraction of sand in the canyon head sediments (400 m, C/N: 10.2; Sand content: 9%) and western wall (900 m, C/N: 12.1; Sand content: 10%) contrasting with the eastern flank and slope that are characterised by finer sediments and more labile organic matter (C/N: 8-10.5; Sand content: 0%) (Zúniga et al., 2009; Romano et al., 2013).

2.4.3.2 Suprabenthic assemblages

A total of 37764 specimens were ascribed to 138 taxa. The amphipods (50.7% of total abundance, 75 species) were the most abundant and species-rich group. The most representative amphipod families were the Eusiridae (predators on zooplankton), Oedicerotidae (predators on meiofauna) and Lysianassidae (scavengers). The mysids (omnivores) were also abundant but showed much lower number of species (33.1%, 11 species). Cumaceans (mostly microbial grazers) and isopods (mostly Munnopsidae, omnivores) had intermediate values of abundance and number of species (5.8% and 33 species; 10.3% and 17 species, respectively) and the less represented groups were tanaids and lophogastrids (0.1%, 1 species each). The peracarids were concentrated in the near-bottom water layer (10-50 cm) (73.8% of the total abundance) and markedly decreased in the upper water layers (55-95 cm and 100-140 cm). This vertical distribution was observed for the amphipods, cumaceans and isopods in most of the sites but the mysids showed higher densities in the upper water layers in several sites.

Except for Rocassa and Sot, the lowest densities were observed in the early spring of 2003 (minimum of 8.5 ind.100 m^{-2} in Mar03 at BaranaS) and the highest in the late spring of 2004 (maximum of 515.6 ind.100 m^{-2} in May04 at L3). Densities were more variable in the canyon sites (Rocassa and Sot) and western slope (L3) mostly owing to fluctuations in the dominance of mysids and amphipods. Overall, sites in the eastern slope (BaranaS and L5) showed much lower densities than the other sites at, or much closer to, the canyon (Fig. 2.4.2, Table. 2.4.2). This difference was statistically significant (Kruskal-Wallis test on average values from Rocassa, Sot and BaranaS, *KS*=6.615, 2 df, $p<0.05$). Amphipods were frequently the most abundant group in all sites and sampling occasions. In turn, mysids showed also important contributions, especially in the canyon (Rocassa and Sot) or nearby canyon (L3) sites where they were occasionally dominant (e.g. Rocassa and Sot in Nov03) (Fig. 2.4.2 and Table.

2.4.2). There was no clear temporal pattern in abundance of the suprabenthos (Kruskal-Wallis on average values for each sampling occasion in Rocassa, Sot and BaranaS, *KS*=3.000, 3 df, $p>0.05$) but when mysids (highly motile component of the suprabenthos) were considered separately, temporal differences in their abundance were statistically significant (Kruskal-Wallis on average values for each sampling occasion in Rocassa, Sot and BaranaS, KS=7.051, 3 df, $p<0.05$). The lowest abundances of mysids were observed in Mar03, while the highest occurred in Nov03 and May04 following the increased particle fluxes observed during autumn and winter.

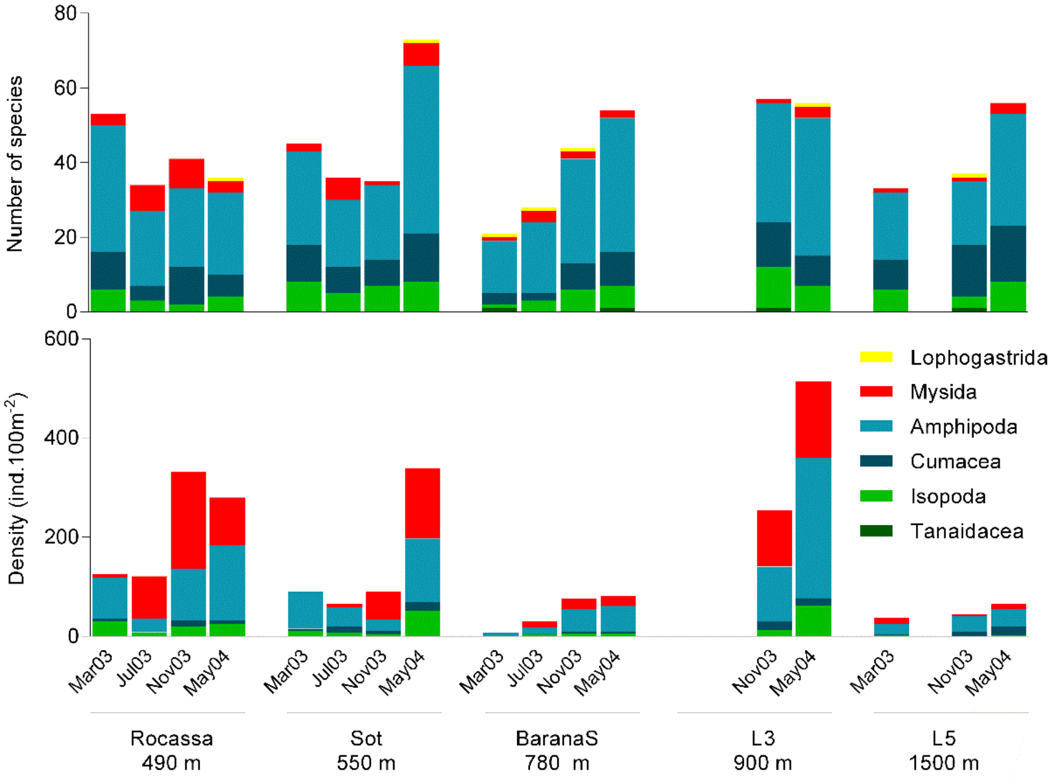

Figure 2.4.2 Number of species and density (ind.100 m^{-2}) of suprabenthic fauna collected in the study sites during the period between March 2003 and May 2004.

Table 2.4.2 Abundance and biodiversity (taxonomic and trophic) data of the suprabenthic assemblage (peracarids only) for the study sites in each sampling occasion during the period between March 2003 and May 2004. N: abundance; D: density; S: number of species; TG: number of trophic groups; H': Shannon-Wiener index (ln-based); J': Pielou evenness index; $ES_{(100)}$ / $ETG_{(100)}$: Hurlbert's expected number of species / trophic groups for 100 individuals.

			Taxonomic diversity				**Trophic diversity**			
Site or Station	**N**	**D (ind.100m^{-2})**	**S**	**H'**	**J'**	**$ES_{(100)}$**	**TG**	**H'**	**J'**	**$ETG_{(100)}$**
RocassaMar03	2430	125.8	53	2.71	0.682	22	14	1.77	0.67	9.3
RocassaJul03	1348	121.3	34	1.92	0.544	15.9	10	1.06	0.46	6.6
RocassaNov03	2572	330.7	41	2.01	0.542	16.4	11	1.3	0.542	7.4
RocassaMay04	3872	280	36	2.3	0.643	17.3	10	1.8	0.781	8.5
SotMar03	1864	89.9	45	2.23	0.586	18.6	13	1.6	0.625	8
SotJul03	1099	65.9	36	2.65	0.739	20.2	10	1.86	0.806	8.1
SotNov03	1020	90.8	35	1.75	0.493	18.4	12	1.38	0.555	9.4
SotMay04	5193	339.2	73	2.92	0.681	25.5	14	1.77	0.672	9.9
BaranaSMar03	98	8.5	21	2.53	0.832	21.0*	10	1.95	0.846	10.0*
BaranaSJul03	420	31.5	28	2.38	0.714	20.3	11	1.79	0.748	9.7
BaranaSNov03	1284	76.2	44	2.77	0.732	24.3	13	1.88	0.735	10
BaranaSMay04	1228	81.2	54	2.87	0.719	25.6	15	1.88	0.695	10
L3Nov03	3416	255	57	2.33	0.577	21.2	14	1.7	0.642	9.5
L3May04	8466	515.6	56	2.39	0.594	19.5	14	1.85	0.7	9.4
L5Mar03	1096	37	33	2.07	0.591	16.7	11	1.41	0.587	6.6
L5Nov03	1026	44	37	2.53	0.7	21.9	12	1.54	0.622	8.4
L5May04	1332	65.6	56	3.01	0.748	26.7	12	1.61	0.646	7.3

***calculated for 98 individuals**

The trophic structure of the assemblages (Fig. 2.4.3) showed both spatial and temporal fluctuations: i) higher relative contribution of fauna relying on water-column/epibenthic food sources (e.g. most mysids, Ep-Om, and eusirid amphipods, EP-Pr-zoo) at Rocassa and L3, the sites subjected to more persistent energetic conditions; ii) dominance of highly motile groups at Sot (scavenging lysianassid amphipods, SR-Sc, in Mar03 and Jul03; mysids, Ep-Om, in Nov03 and May04); iii) higher relative contribution of fauna relying on benthic food sources (e.g. Oedicerotidae amphipods, SR-Pr-mei; Munnopsidae isopods, SR-Om) at Barana and L5 in the eastern slope; iv) increased relative contribution of zooplankton predators (eusirid and synopiid amphipods, EP-Pr-zoo) and microbial grazers (cumaceans, SR-Gr-mic) towards greater depths (namely in L5 at 1500 m depth).

The highest dominances (Supplementary Material, Table. S2.4.1) were observed in the canyon sites: the mysid *Hemimysis abyssicola* (Ep-Om) was the dominant species in Rocassa (up to 49.3% of the total abundance observed in Jul03) while in Sot the amphipod *Scopelocheirus hopei* (SR-Sc) and the mysid *Boreomysis arctica* (Ep-Om) alternated in the dominant position (*S. hopei*: 40.2% in Mar03; *B. arctica*: 63.3% in Nov03). The mysid *B. arctica* also dominated in L3 (reaching 44.8% in Nov03). BaranaS (most dominant species: 24.5-36.7%) and L5 (14.8-33.6%) presented lower dominances shared between the mysid *B. arctica* and several amphipods: in BaranaS, the stegocephalid *Mediterexis mimonectes* (Sr-Dt), the oedicerotids *Bathymedon longirostris* and *B. acutifrons* (SS-Pr-mei) and in L5, also *B. longirostris* and the eusirid *Rhachotropis caeca* (EP-Pr-zoo).

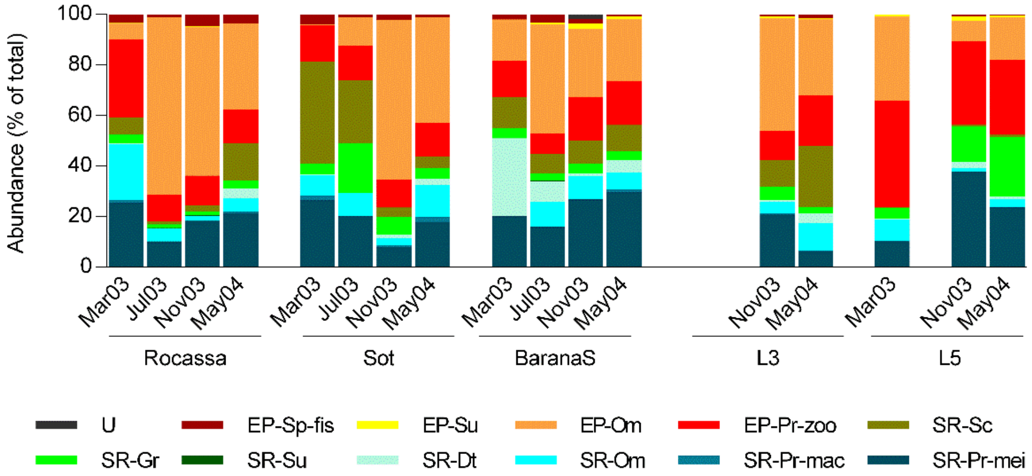

Figure 2.4.3 Relative abundance (%) of trophic groups in the suprabenthos from the study sites throughout the sampling period (March 2003 – May 2004) - simplified trophic scheme (some less represented groups were pooled together). The trophic code is based on the food source (EP: water column food sources, SR: sediment surface or subsurface food sources), feeding mode (Om: omnivores; Dt: Detritus feeder, Su: Suspension/Filter feeder, Pr: Predator, Sc: Scavenger, Sp: Suctorial parasite, Gr: Grazer) and food type and size (mic: microfauna; mei: meiofauna; mac: macrofauna; zoo: zooplankton).

Biodiversity trends were much less clear. Overall, the highest number of mysid species occurred at Rocassa (8 in Nov03) while the deeper sites showed the highest number of amphipod (L3 in May04: 37), isopod (L3 in Nov03: 11) and cumacean species (L5 in May04: 15). The minima of taxonomic and trophic diversity were observed in Jul03 and Nov03 at Rocassa (taxonomic - H': 1.92-2.01, J': 0.542-0.544, $ES_{(100)}$: 15.9-16.4; trophic - H': 1.06-1.30, J': 0.460-0.542, $ETG_{(100)}$: 6.6-7.4; Table 2.4.2). This site also showed the most important temporal changes in trophic diversity expressed by the highest observed values of β-diversity for TG and ETG$_{(100)}$ (25.0 and 10.1%, respectively, Table 2.4.3). Despite yielding the lowest densities and number of species (21 in Mar03 and 28 in Jul03), BaranaS showed a high turnover in the number of species and trophic groups (β-diversity: 50.3 and 23.4%, respectively, Table 2.4.3), which resulted in consistently higher values of taxonomic (H’: 2.38-2.87; J’: 0.714-0.832; ES$_{(100)}$: 20.3-25.6) and trophic diversity (H’: 1.79-1.95; J’: 0.695-0.846 and ETG$_{(100)}$: 9.7-10.0) (Fig. 2.4.2 and Table 2.4.3). Sot was characterised by large temporal fluctuations in community structure reflected in higher values of β-diversity for ES$_{(100)}$ and ETG$_{(100)}$ (16.5 and 9.7%, respectively, Table 2.4.3); this site showed the maximum number of species (73) and high taxonomic diversity (H’, ES$_{(100)}$) in May04, but also the minimum H’ and J’ (1.75 and 0.430, respectively) in Nov03. L5 also showed important temporal fluctuations, although within lower values of density and number of species; this site showed the maximum values of H’ and ES$_{(100)}$ (3.01 and 26.7, respectively) in May 04, but also low values of H’, ES$_{(100)}$ and ETG$_{(100)}$ in Mar 03 (Table 2.4.2).

Table 2.4.3 Overall abundance and biodiversity data of the suprabenthic assemblage (peracarids only) in each study site (pooled samples over the study period). N: abundance; S: number of species; TG: Number of trophic groups; ES$_{(100)}$ / ETG$_{(100)}$: Hurlbert’s expected number of species / trophic groups for 100 individuals.

	N	S	Diversity partition (%)		ES$_{(100)}$	Diversity partition (%)		TG	Diversity partition (%)		ETG$_{(100)}$	Diversity partition (%)	
			α	β		α	β		α	β		α	β
Rocassa	10222	83	49.4	50.6	20.0	89.1	10.9	15	75.0	25.0	8.7	89.9	10.1
Sot	9176	86	54.9	45.1	24.8	83.5	16.5	14	87.5	12.5	9.8	90.3	9.7
BaranaS	3030	74	49.7	50.3	28.9	85.2	14.8	16	76.6	23.4	10.5	97.6	2.4
L3	11882	79	71.5	28.5	21.7	95.0	5.0	16	87.5	12.5	9.6	97.3	2.7
L5	3454	70	60.0	40.0	24.7	90.0	10.0	14	83.3	16.7	7.7	96.6	3.4

When the taxa with more affinity to the sediment (amphipods, cumaceans and isopods) are considered separately, the assemblage appears to respond with an increased biodiversity (ES$_{(50)}$) in Nov03 and May04, following the increased particle fluxes during autumn and winter (Fig. 2.4.4). This happens in fished and non-fished areas, on the canyon flanks and at the slope; the exception is Rocassa (head of the canyon) where values were consistently low and a slight decrease in ES$_{(50)}$ was observed. The more motile component of the suprabenthos (mysids) does not show such temporal patterns.

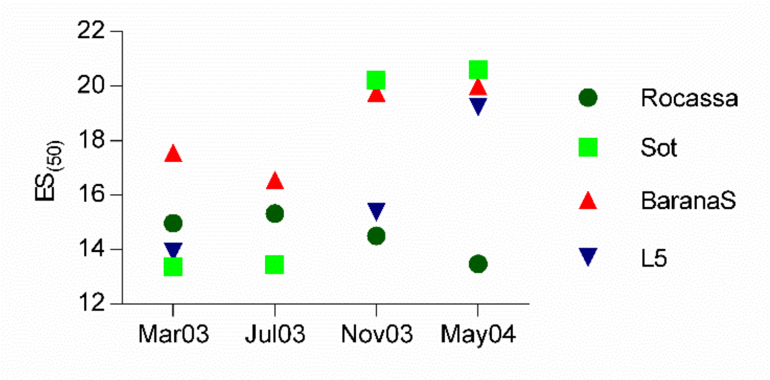

Figure 2.4.4 Variation of Hurlbert's expected number of species (ES_{50}) throughout the study period (March 2003 – May 2004) showing the putative response of peracarids (mysids excluded) to the increased particle fluxes in autumn and winter 2003-04. Note: Site L3 is not shown because it was sampled only twice.

2.4.3.3 Multivariate analyses

The MDS plot (Fig. 2.4.5) shows the study sites in a gradient of increasing distance to the canyon along the horizontal axis (from Rocassa in the left to L5 and BaranaS in the right). There is also a clear segregation according to both the depth-related influence of water masses (Rocassa and Sot, influenced by LIW, separated from L3, BaranaS and L5, influenced by the WMDW) and the occurrence of trawling, with the fished areas at the top of the plot and non-fished areas at the bottom (Fig. 2.4.5). The ANOSIM tests (Table 2.4.4) showed highly significant differences for the factor "water masses" (ANOSIM test 1, R= 0.635; P=0.1%) and very significant differences for the factor "fishing pressure" (ANOSIM test 2, R= 0.339; P=1.4%), but no statistically significant temporal differences (Table 2.4.4, ANOSIM test 3). The fished sites are the shallower ones - Rocassa and Sot under the influence of LIW and BaranaS under the influence of WMDW. Therefore, there is an important overlap of the two factors which is reflected by the SIMPER results (Supplementary material, Table S2.4.2): the most relevant contributors for the similarity within "LIW" and "Fished" are the same (the mysid *Boreomysis arctica*, the amphipods *Scopelocheirus hopei* and *Synchelidium haplocheles* and the isopod *Munnopsurus atlanticus*) and the ones for "WMDW" and "Non-fished" are also the same (*B. arctica* and the amphipods *Rhachotropis caeca*, *Bathymedon longirostris* and *Bathymedon banyulsensis*). The fact that the sites under the influence of the LIW are also the ones under a greater influence of the canyon environment and that there are no replicates at the same depth for fished and non-fished areas are important caveats to the interpretation of these analyses. Additionally, the “Non-fished” sites were not visited in all sampling occasions.

Table 2.4.4 Results of the ANOSIM one-way analyses the factors “water masses”, “fishing pressure” and “time”.

	Sample Statistic	**Permutations used**	**Significant statistics**	**P**
Anosim test 1: water masses (LIW vs. WMDW)				
Global value	0.635	999	0	0.1**
Anosim test 2: fishing pressure (fished vs. non-fished)				
Global value	0.339	999	13	1.4*
Anosim test 3: Time (sampling occasion)				
Global value	0.093	999	176	17.7ns

*Significant; **Very Significant; ns: not significant.

A more coherent analysis was performed by using a subset of the data including only Rocassa, Sot and BaranaS fishing grounds which were sampled in the four sampling occasions. Spatial and temporal changes in the assemblages subjected to fishing impacts were assessed. Significant differences were found among sites (Table 2.4.5, ANOSIM Test 2, Global R: 0.637; P: 0.1%) but not among sampling occasions (Table 2.4.5, ANOSIM Test 1). SIMPER analyses indicate several dominant species as the most relevant contributors both for the similarity within and the dissimilarity between sites (Supplementary material, Table S2.4.3). The dominant species in Rocassa, *Hemimysis abyssicola* (mysid, Ep-Om), is the most important contributor for the similarity within this site and its dissimilarity in relation to Sot and BaranaS where the species is mostly absent. The dominant species in Sot and BaranaS, *Boreomysis arctica* (mysid, Ep-Om), is the most important contributor to the similarity within BaranaS and for the dissimilarity between Sot and the other two sites. The low abundances in BaranaS of the amphipods *Synchelidium haplocheles* (SR-Pr-mei, second most dominant species in Rocassa) and *Scopelocheirus hopei* (Sr-Sc, second most dominant species in Sot) also have a high contribution for the dissimilarity between BaranaS and the other two sites.

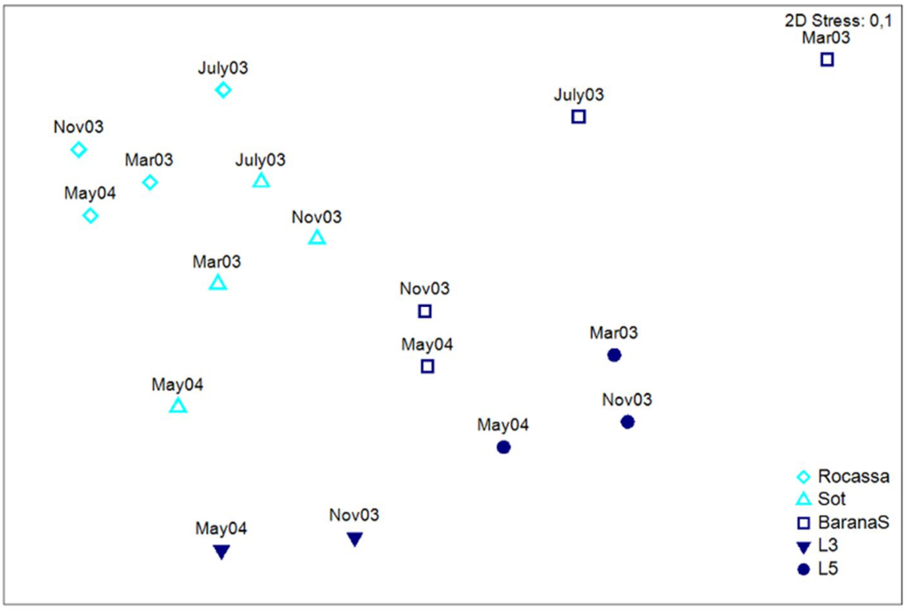

Figure 2.4.5 MDS (multidimendional scaling) 2D ordination plot based on Bray Curtis similarity (density data expressed as ind.100 m^{-2}) of the suprabenthic assemblages collected in the Blanes canyon region in the period between March 2003 and May 2004. Open symbols: fished areas; Full symbols: non-fished areas; Light blue: sites under the influence of the Levantine Intermediate Water; Dark blue: sites under the influence of the Western Mediterranean Deep Water.

Table 2.4.5 Results of the ANOSIM one-way analysis for global and pairwise tests for the factor “time” (ANOSIM test 1) and “area” (ANOSIM test 2) for Rocassa, Sot and BaranaS. MDS not showed because is similar for the one obtained for all of the sampled sites.

	Sample Statistic	Permutations used	Significant statistics	P
Anosim test 1: Time				
Global value	-0.028	999	565	56.6ns
Anosim test 2: Site				
Global value	0.637	999	0	0.1**
Pairwise tests				
Rocassa, Sot	0.698	35[a]	1	2.9*
Rocassa, BaranaS	0.719	35[a]	1	2.9*
Sot, BaranaS	0.549	35[a]	1	2.9*

[a] all possible permutations.

*Significant; **Very Significant; ns: not significant.

2.4.3.4 Fishing regime

The available data on the rose shrimp fisheries (from January 2002 to July 2004) indicate that there is a strong relationship between the monthly values of biomass landed (kg.mo^{-1}) and the fishing effort (trawling time, h.mo^{-1}). The higher slope coefficients of the linear regressions for Barana (11.8) and Cara Norte (10.1) further indicates that the CPUEs were higher in these two fishing grounds, where most of the fishing effort is allocated, than in Cabecera (7.7) (Fig. 2.4.6). However, these differences are not so clear during the period coincident with this study (values from January 2003 to July 2004 plotted in Fig. 2.4.7) when the CPUE ranged mostly within 5 and 12 kg.h^{-1}, with peaks of over 15 kg.h^{-1} in April 2003 (17 in Barana, 18.5 in Cabecera) and May 2004 (15 in Barana).

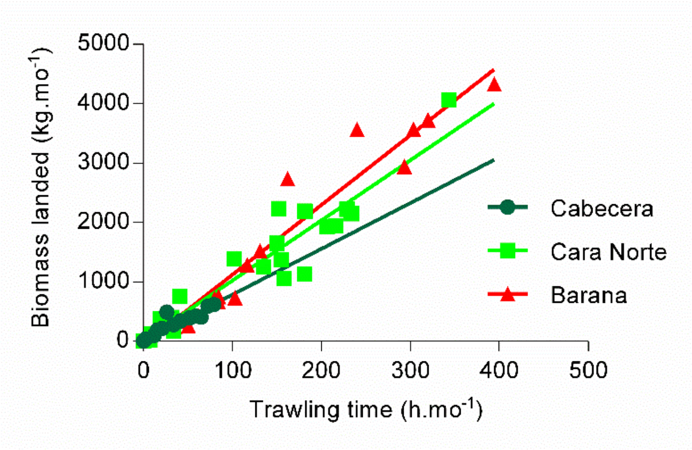

Figure 2.4.6 Relationship between monthly values of shrimp capture and trawling time in the three fishing grounds illustrating the overall higher CPUE in Barana and Cara Norte.

In terms of fishing pressure (kg of biomass landed per km^2 or trawling time per km^2, Fig. 2.4.7), Cabecera is the least impacted fishing ground (biomass removed and trawling time always <8 kg.km^{-2} and <1 h.km^{-2}, respectively, mostly during autumn and winter), while Barana is subjected to much higher fishing pressure but only seasonally in spring and early summer (reaching 26.7 kg.km^{-2} and 2.4 h.km^{-2}) and Cara Norte is subject to a more continued fishing regime, with high pressure especially in the winter (reaching 22.4 kg.km^{-2} and 2.4 h.km^{-2}) and summer (reaching 40.9 kg.km^{-2} and 3.5 h.km^{-2}).

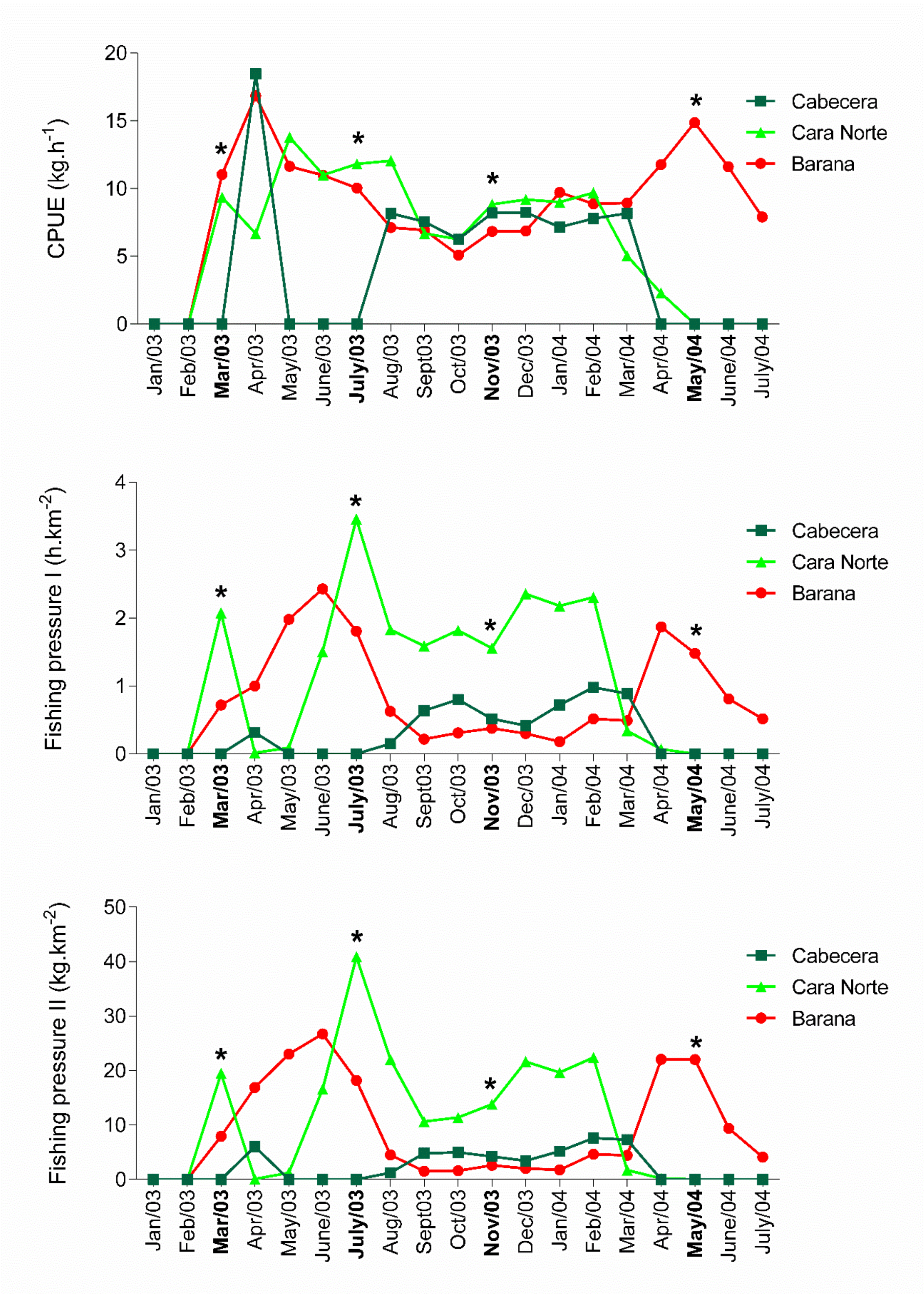

Figure 2.4.7 CPUE and fishing pressure (accumulated by month) in the fishing areas Cabecera (81 km^2), Cara Norte (99 km^2) and Barana (162 km^2) from January 2003 to July 2004. Months in bold and asterisk correspond to the suprabenthic sampling occasions.

When density and diversity indices of the suprabenthic assemblages are plotted against fishing pressure (average of the 3-month period before suprabenthos sampling, Fig. 2.4.8), no trends are evident in Rocassa (Cabecera fishing ground) and BaranaS (Barana fishing ground) where fishing occurs only seasonally. Sot assemblages (Cara Norte fishing ground), subjected to a more continuous fishing regime throughout the year, appears to show a decrease in density, number of species and number of trophic groups with increasing fishing pressure, while the other biodiversity indices reach their lowest values for intermediate values of fishing pressure (suggesting and inverted hump-shaped curve). While in Rocassa and BaranaS the number of species and density increase in Nov03 and May04 under favourable environmental conditions (Fig. 2.4.2), a similar trend in Sot is only observed in May04 when fishing pressure is relieved. In Jun03, under the highest fishing pressure, the lowest density and number of species observed in Sot are accompanied by an increase in the taxonomic and trophic evenness of the suprabenthos, which leads to higher biodiversity estimates. In this sampling occasion the scavenging amphipod *Scopelocheirus hopei* is the dominant species, but accounts only for 23.7% of the total abundance (Supplementary Material Table S2.4.1).

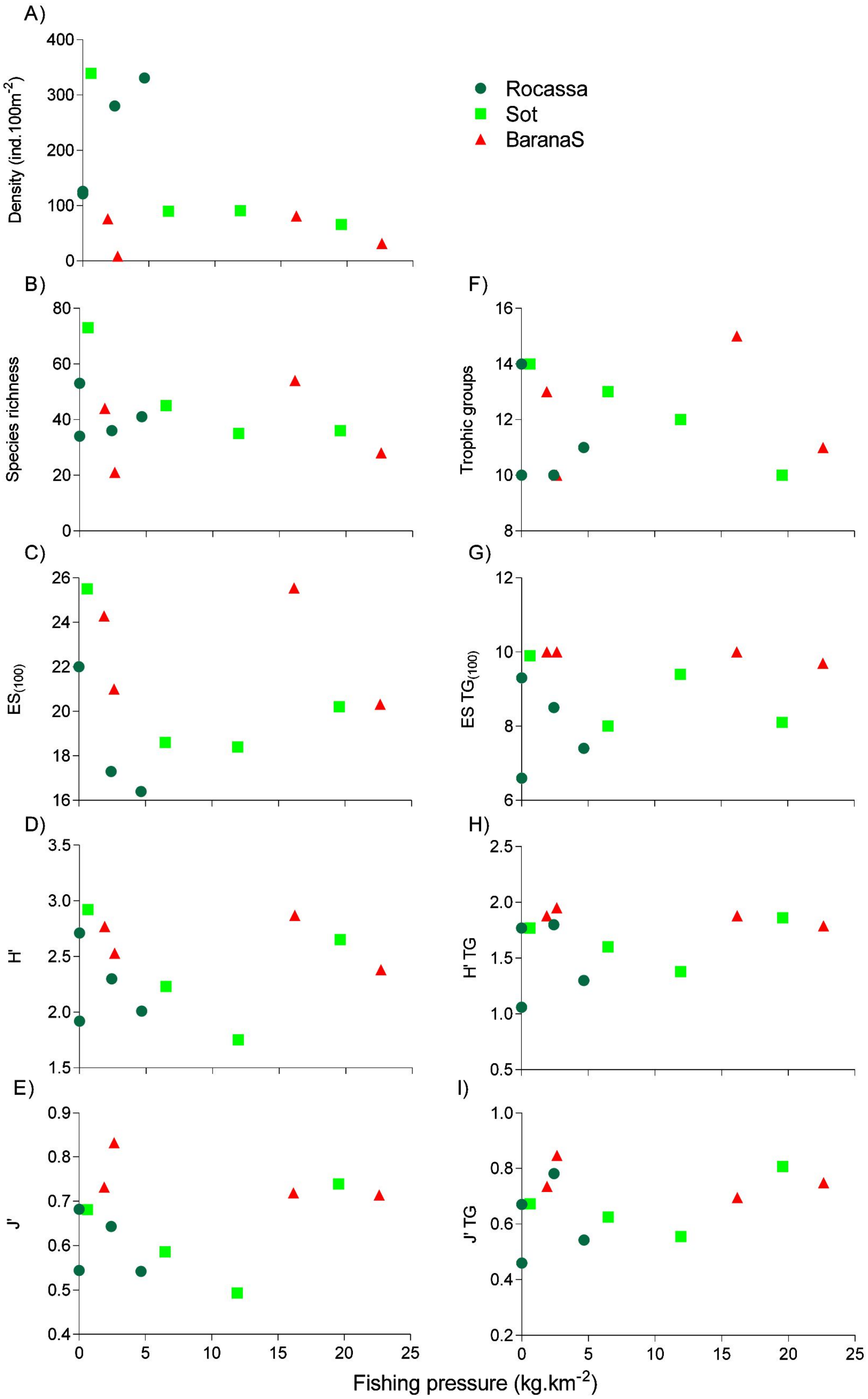

Figure 2.4.8 Density and biodiversity (taxonomic – B) C) D) E); trophic – F) G) H) I)) in relation to fishing pressure (monthly values of biomass removed, kg.km^{-2}). The sites Rocassa, Sot and BaranaS are located in Cabecera, Cara Norte and Barana, respectively. ES$_{(100)}$: expected species number for 100 individuals, *H'*: Shannon-Wiener diversity; *J'*: Pielou evenness index. TG: trophic groups.

2.4.4 Discussion

Traditionally viewed as a physically stable environment, the deep sea is in fact disturbed by various processes, some periodic and other irregularly pulsed, which may involve phytodetritus deposition, high current speeds, benthic storms, atmospheric driven events (e.g. dense shelf-water cascading) and human activities (e.g. trawling) (Lampitt, 1985; Thistle et al., 1985; Canals et al., 2006; Company et al., 2008; Puig et al., 2012). Several of these sources of spatial and temporal oceanographic variability characterize the continental margin in the NW Mediterranean, where they have a relevant impact on the biodiversity and structure of the benthic (Mamouridis et al., 2011; Romano et al., 2013; Pusceddu et al., 2014), mega-epibenthic (Company et al., 2008; Ramírez-Llodrà et al., 2009; Sardà et al., 2009; Tecchio et al., 2013) and suprabenthic assemblages (this study).

Previous studies on the suprabenthos, covering a bathymetric range of 249-1620 m depth, identified distinct assemblages in the Balearic slope and in the Catalan Sea in relation to the influence of the different water masses in the NW Mediterranean (Cartes et al., 2003, 2011). Accordingly, the multivariate analysis of our data indicated the most significant differences in the composition and structure of the suprabenthic assemblages when the samples were grouped in two depth ranges relative to the influence of the LIW and WMDW water masses. Unfortunately, as it often happens during deep-sea multidisciplinary cruises, time and resource constraints compromised an optimal sampling design with adequate replication. This relevant caveat hindered a clear distinction of the influence of depth as a proxy for water mass properties, the canyon effect and the fisheries impact on the suprabenthic crustacean assemblages. Nevertheless, there are important patterns in the abundance and biodiversity of these assemblages that can be related to the natural disturbance and fishery regimes, which are discussed below.

2.4.4.1 Environmental variables and natural disturbance

Studies on deep-sea suprabenthos are not as common as on other benthic assemblages. This biological component shows typically high spatial and temporal variability in abundance and species composition, which complicates any possible comparisons. In temperate regions, suprabenthos has been mostly studied in the NE Atlantic and western Mediterranean continental slopes, rarely extending to depths greater than 1000 or 2000 m. In the southern Bay of Biscay suprabenthic assemblages in canyon areas have been studied in Cap Ferret Canyon (346–3070 m depth; e.g. Elizalde et al., 1993; Dauvin et al., 1995), Capbreton Canyon (158–1000 m depth; e.g. Frutos et al., 2012; Frutos and Sorbe, 2014) and Avilés Canyon (207–1024 m depth, Frutos et al., 2012), showing a general decrease in suprabenthic densities with increasing depth. This is a well-known trend in deep-sea benthic communities (Rex et al., 2006). However, the usual decrease in density (and biomass) with increasing depth and distance from coast is frequently altered by the occurrence of canyons and our results indicate significant higher densities of suprabenthos from canyon sites (Rocassa and Sot) than from the slope (BaranaS).

The particular conditions in current regimes and sediment transport in canyons tends to concentrate organic matter in terraces and other depositional areas, leading to high temporal and spatial heterogeneity and favouring the localised occurrence of higher densities and/or biomass of benthic fauna (Bianchelli et al., 2010; Cunha et al., 2011; Romano et al., 2013; Tecchio et al., 2013). In our study, maximum densities of suprabenthic crustaceans were observed at 900 m depth (site L3), in agreement with previous studies on suprabenthos from the NW Mediterranean that have shown maximum abundances and/or biomasses occurring around 1000 m depth in the Catalan slope (Cartes et al., 2003). Cartes et al. (2010) relate the occurrence of these maxima to favourable trophic conditions at this depth associated to the current regimes, vertical sinking and advective processes of organic matter transport. The observed suprabenthic densities were in general one order of magnitude lower in L5 (the deepest site at 1500 m depth) and BaranaS (the most distant from the canyon) both in the eastern slope. This variability is within the range of spatial patterns observed in suprabenthos studies in various contexts, other than the occurrence of canyons (e.g. Cartes, 1998).

The spatial and temporal patterns in suprabenthic densities may be related to the hydrodynamic and particle flux regimes in the Blanes Canyon region. Higher densities occurred at the canyon head and western slope, which appear to be the preferential routes for the water masses and particle fluxes, while in the adjacent eastern slope observed particle fluxes were several orders of magnitude lower (Zúniga et al., 2009). Over the time, an overall increase in density was observed in Nov03 and May04 (particularly significant for the more motile component of the assemblage). These increased densities followed peaks in river discharges with subsequent higher current velocities and particle fluxes in October 2003 and March 2004, reinforced during winter by a moderate dense shelf water cascading event (Palanques et al., 2006; Zúniga et al., 2009). As noted by Cunningham (2005) the energetic conditions, affecting primarily the canyon, can have sufficient magnitude to overspill and lead to organic matter enrichment also in the surrounding areas.

Suprabenthic assemblages from the NE Atlantic (continental slope of the Bay of Biscay, Sorbe and Elizalde, 2014) clearly show seasonal patterns related with spring phytodetritus deposition. In the Catalan slopes, the energetic hydrodynamic events responsible for mobilising large amounts of nutritive and fresh organic matter, may override the effect of such seasonal fluxes derived from the surface productivity (Ramírez-Llodrà et al., 2008; Sanchez-Vidal et al., 2008; Mamouridis et al., 2011; López-Fernández et al., 2013) as the main driver of temporal fluctuations in the abundance and biomass of biological assemblages. The faunal response may occur with a delay of 0-2 months depending on the trophic level (Cartes et al., 2003, 2010; Papiol et al., 2012). Nevertheless, higher inputs of organic matter associated to the winter-spring and autumn phytoplankton blooms (Estrada, 1996) may further support the generalised seasonal increase in abundance of the suprabenthic assemblages observed in May04 both in canyon and slope sites.

Understanding the spatial and temporal fluctuations in abundance, and especially in dominance, is crucial for the interpretation of biodiversity patterns. In the Balearic Islands, fluctuations in diversity of suprabenthic assemblages were interpreted in relation to the influence of frontal systems and flow dynamics associated to different water masses (Cartes et al., 2011). But in fact, different components of the suprabenthic assemblage may respond differently to environmental drivers often resulting in complex biodiversity patterns as shown by our results: i) the dominant species were mostly highly motile mysids and amphipods and played the main role in the spatial and temporal dynamics of the community structure; ii) the temporal variations in hydrographic and trophic conditions were apparently coupled with significant fluctuations in mysid densities, while the remaining peracarids portrayed significant changes in biodiversity.

The highly motile component of the suprabenthos, which includes mysids and predatory and scavenging amphipods, may respond very rapidly with large fluctuations in density to changes in oceanographic conditions (e.g. current speed, temperature) and food availability (e.g. Vicente and Sorbe, 1995; Sorbe 1999; Kaiser et al., 2007). On the other hand, the less motile suprabenthos component with higher affinity to the sediment (other amphipods, most isopods and cumaceans) is more susceptible to physical disturbance and may respond in terms of biodiversity to food quality rather than quantity (Cunha et al., 2011); their distribution are usually correlated with the sedimentary properties of the habitat, which integrate environmental conditions over time.

Relevant hydrodynamic disturbance events, such as near-bottom currents over 15-20 cm.s^{-1} capable of resuspending and redistributing sediments at the seafloor, tend to be more frequent and intense at the upper reaches of canyons and are a major driver structuring the benthic assemblages (Thistle et al., 1985; Aller, 1997; Levin et al., 2001). Sediment mobility and reworking as a consequence of periodical disturbance by erosive flows creates repeated opportunities for recolonization, ensuring that faunal assemblages remain in a high dominance/low diversity, early successional state (Lambshead et al., 1983; Thistle et al., 1985; Levin et al., 2001). This is in agreement with the low diversity and higher turnover (β-diversity) observed in the Blanes Canyon head (and, to a lesser extent, also in the western flank) where erosion processes are more active (Zúñiga et al., 2009), contrasting with the higher diversity values observed in the sedimentary more stable eastern slope.

Intense physical disturbance in canyons is often coupled with organic enrichment (De Leo et al., 2010) and select for more motile (and often larger sized) species that are able to forage more efficiently in an unstable environment. These conditions may explain the high turnover in the trophic structure of the assemblage in the canyon head (which is the area most affected by temporal fluctuations of river discharges) and the overall high dominance of omnivore mysids (*Hemimysis abyssicola* and *Boreomysis arctica*), scavenger lysianassids (*Scopelocheirus hopei)* and zooplankton-predator eusirids (*Rachothropis* spp.) in the canyon or near-canyon sites. With increasing distance from the canyon (BaranaS) and depth (L5), the sedimentary environments are steadier, with finer grain sizes and molar C/N values around 8 that indicate the high quality and predominantly marine origin of the organic matter. These conditions may explain the substantially higher relative contribution of less motile groups that explore sediment food sources, such as predators on meiofauna (*Bathymedon* spp.), microbial grazers (cumaceans), surface omnivores (*Munnopsurus atlanticus*) and detritivores (*Mediterexis mimonectes*) found in these sites despite their overall low densities.

2.4.4.2 Trawling disturbance

Deep-sea trawling fisheries target predominantly seamounts (Clark et al., 2015) and canyon flanks (Stefanescu, 1994; Company et al., 2012; Miller et al., 2012), where large aggregations of species with commercial interest often occur. Physical alteration or loss of seafloor habitats (e.g. decreased structural complexity, higher re-suspension rates), increased mortality of target and non-target populations, and increased food availability (e.g. discards, higher vulnerability of incidentally harmed organisms to predators and scavengers) are the main direct effects of trawling. Indirect effects are selective biomass removal, changes in overall community structure and size spectrum, species interactions and, ultimately, alterations in the trophic webs and in the flow of materials and energy through ecosystems (NRC, 2002). Because of their proximity to the mainland, systems like the Blanes Canyon are areas of intense natural disturbance but also particularly exposed to fishing (Company et al., 2012; Puig et al., 2012).

Our results show significant differences among the suprabenthos assemblages from the three fishing grounds in the Blanes Canyon region. The magnitude and duration of the effects of trawling is known to depend not only on the fishing gear (e.g. configuration, towing speed) but also on the prevalence and intensity of fishing and on the habitat fished (e.g. substrate type, depth, biological structure) (NRC, 2002). In the sites where fishing effort showed marked seasonality, Rocassa (Cabecera) and BaranaS (Barana), spatial differences and temporal changes in the biodiversity and structure of the suprabenthos were closely related to the natural disturbance regime (section 4.1 above). However, the pattern of high temporal fluctuations in Sot (Cara Norte) may be better explained in relation to the high and more continued fishing pressure.

Species richness and abundance in Sot showed a decline with increasing fishing pressure, a trend that is often related to the elimination of more vulnerable species and maintenance of reduced populations of bathyal benthic communities under repeated or persistent trawling (Clark et al., 2015). Noteworthy, is that low species richness and abundance were rapidly reverted in May04 when fishing pressure was relieved and other environmental conditions were also favorable. In fact, although exacerbated effects of trawling on deep-sea assemblages and slow recovery may be expected, because of life history traits such as low growth rates, high longevity, delayed reproduction and low natural mortality (Pickett and White, 1995; Thrush and Dayton 2002), these effects are not consistent across deep-sea habitats or biological compartments subjected to trawling (Kaiser et al., 2006; Atkinson et al., 2011). For instance, increased epibenthic abundance and diversity was observed in the shelf break and upper slope of the Tyrrenian Sea (Mangano et al., 2013), while decreased epifaunal abundance, species richness and diversity were found together with no differences for the infauna in the upwelling Benguela region (Atkinson et al., 2011); in the NE Irish Sea, negative effects on species richness and abundance of the infauna were detected (Hinz et al., 2009; Romano pers. communication) and the meiofauna from canyons showed reduced abundance and diversity (Pusceddu et al., 2012) or no differences in species richness, together with changes in community structure and vertical distribution (Leduc and Pilditch, 2013). Noteworthy, is that the lowest trophic and taxonomic diversity in Sot was observed under intermediate levels of fishing pressure maybe because by keeping low population levels across all species, higher pressure levels in Jun03 may increase evenness and lead to higher biodiversity estimates.

Changes in the dominant species related to fishing pressure are scarcely addressed in literature. In Sot, the dominance of *Scopelocheirus hopei* is possibly a response to additional food sources, such as discards and biota killed or damaged by trawling that likely attract predators and scavengers (Fanelli et al., 2009; Dannheim et al., 2014). The amphipod assemblage from Merenguera Canyon (Cartes and Sorbe, 1999), another NW Mediterranean canyon region subjected to trawling, was occasionally dominated by *S. hopei*, but also by infaunal species (*Carangoliopsis spinulosa* and *Harpinia* spp.). Below 1000 m depth, the limit of fishing activity, the dominant species from Merenguera and Blanes canyons were more similar. It has been suggested that the prolonged and intensive fishing activity in the Blanes area (over seven decades) may partly explain the differences between the biological assemblages from these two close regions (Ramírez-Llodrà et al., 2009; Sardà et al., 2009). But then, again, the evaluation of trawling effects is complicated by the lack of historical data, especially before fishing began. In fact, the spatial and temporal scales of trawling represent novel selective pressures for the bathyal biological assemblages that, in areas intensively trawled for decades like Blanes Canyon (this study) or the Tyrrenian Sea (Mangano et al., 2013), may already show a profoundly altered state of adaptation (Hall, 1999).

2.4.4.3 Final remarks

Both natural and anthropogenic disturbances can occur with different periodicities, spatial effects, and patterns of recovery. The resilience (Holling, 1973) of a system (degree to which an ecosystem's long-standing composition, structure, and function can recover from disturbance) depends on thresholds of intensity and/or prevalence of the disturbance, but also on the characteristics of the species affected. Short-lived, highly motile or dispersing species with high reproduction rates will recover from disturbance faster than the ones with opposite traits (Pickett and White, 1995).

Therefore, we can expect suprabenthos to show high resilience to trawling disturbance, even more in areas such as the Blanes Canyon where the assemblages are frequently exposed to natural disturbance at different temporal scales (e.g. strong currents, seasonal river discharges, dense shelf water cascading events). In such cases, the threshold of intensity or cumulative level beyond which persistent changes occur may be higher than for other biological component or in other ecosystems.

The interpretation of changes in biodiversity is further confounded by natural migrations and biotic interactions beyond the scope of this work but that may also be relevant in the study area. For instance, vertical and horizontal ontogenic migrations of mysids are known to occur between canyons and the adjacent slope (Cartes and Sorbe, 1995; Vicente and Sorbe, 1995; Cartes et al., 2010). In the Western Mediterranean, suprabenthic species are relevant items in the diet of megafauna (e.g. Sardà and Cartes, 1997; Carrassón and Cartes, 2002). Cartes et al (2010) suggested a relation between these migratory movements of mysids and the rose shrimp *A. antennatus* aggregations which, in turn, determines temporal changes in the intensity and spatial distribution of the fishing effort by the three fishing grounds (Sardà et al., 2004, 2009; Gorelli et al., 2014). This means that while trawling causes high physical disturbance, it may also induce predation relief. The changes in the biodiversity of suprabenthos resulting from this conjugation of factors will depend on the unknown balance of their effects on dominance and competitive interactions. These may partly explain a pattern in biodiversity (observed in Sot) that apparently contradicts the hump-shaped relationship predicted by the intermediate disturbance hypothesis (Connell, 1978).

Given the extensive new bathyal regions including submarine canyons and seamounts, that have been exposed to the effects of trawling worldwide, the size of the affected fishing grounds and the lack of historical data, a more coordinated and focused effort on future studies is of outmost importance. A better knowledge on the synergies of natural and anthropogenic disturbance regimes, life history traits of different faunal compartments, biotic interactions, trophic structure, and energy-flow alterations will contribute to establish causation and underpin relevant questions on the short- and long-term consequences of deep-sea bottom trawling.

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Supplementary material

Table S2.4.1. Six dominant taxa of suprabenthos collected with a suprabenthic sledge at all the sites in the period between March 2003 and May 2004.

Table S2.4.2. Breakdown of percentual contributions from SIMPER analysis for comparisons between water masses (LIW vs.WMDW) and fishing pressure (fished (F) vs.non-fished areas (NF)).

Table S2.4.3. Breakdown of percentual contributions from SIMPER analysis for comparisons between fishing grounds (Rocassa, Sot, BaranaS).

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Supplementary material

Table S2.4.1 Six dominant taxa of suprabenthos collected with a suprabenthic sledge at all the sites in the period between March 2003 and May 2004.

Rocassa	**Mar03**			**July03**			**Nov03**			**May04**	
SS-Pr-mei	*Synchelidium haplocheles*	20.2	Ep-Om-mic	*Hemimysis abyssicola*	49.3	Ep-Om-mic	*Hemimysis abyssicola*	47.0	Ep-Om-mic	*Hemimysis abyssicola*	30.7
SR-Om-mic	*Munnopsurus atlanticus*	19.7	Ep-Om-mic	*Boreomysis arctica*	16.5	SS-Pr-mei	*Synchelidium haplocheles*	13.6	SS-Pr-mei	*Synchelidium haplocheles*	19.3
EP-Pr-zoo	*Rhachotropis grimaldii*	10.0	SS-Pr-mei	*Synchelidium haplocheles*	8.3	Ep-Om-mic	*Boreomysis arctica*	10.2	SR-Sc-mac	*Scopelocheirus hopei*	14.6
EP-Pr-zoo	*Rhachotropis integricauda*	8.3	SR-Om-mic	*Munnopsurus atlanticus*	4.3	EP-Sp-fis	*Gnathia* sp	4.7	EP-Pr-zoo	*Rhachotropis grimaldii*	4.5
SR-Sc-mac	*Scopelocheirus hopei*	6.1	EP-Pr-zoo	*Rhachotropis grimaldii*	3.3	EP-Pr-zoo	*Rhachotropis grimaldii*	4.7	SR-Om-mic	*Munnopsurus atlanticus*	4.3
Ep-Om-mic	*Hemimysis abyssicola*	4.4	EP-Pr-zoo	*Rhachotropis rostrata*	2.8	EP-Pr-zoo	*Rhachotropis rostrata*	3.1	SR-Dt	*Mediterexis mimonectes*	3.7
		68.6			84.4			83.3			77.2
Sot	**Mar03**			**July03**			**Nov03**			**May04**	
SR-Sc-mac	*Scopelocheirus hopei*	40.2	SR-Sc-mac	*Scopelocheirus hopei*	23.7	Ep-Om-mic	*Boreomysis arctica*	63.3	Ep-Om-mic	*Boreomysis arctica*	22.1
SS-Pr-mei	*Synchelidium haplocheles*	15.3	SS-Pr-mei	*Synchelidium haplocheles*	11.6	SS-Pr-mei	*Synchelidium haplocheles*	3.9	Ep-Om-mic	*Pseudomma affine*	12.2
SS-Pr-mei	*Bathymedon acutifrons*	6.3	SR-Gr-mic	*Leucon longirostris*	10.6	SR-Sc-mac	*Scopelocheirus hopei*	3.5	SR-Om-mic	*Munnopsurus atlanticus*	11.4
SR-Om-mic	*Munnopsurus atlanticus*	5.0	SR-Om-mic	*Munnopsurus atlanticus*	8.4	EP-Pr-zoo	*Rhachotropis rostrata*	3.0	Ep-Om-mic	*Parapseudomma calloplura*	7.0
EP-Pr-zoo	*Bruzelia typica*	4.3	SR-Gr-mic	*Diastyloides serratus*	7.6	SR-Gr-mic	*Leucon longirostris*	2.7	SS-Pr-mei	*Synchelidium haplocheles*	6.5
EP-Sp-fis	*Gnathia* sp	3.6	Ep-Om-mic	*Boreomysis arctica*	6.1	EP-Pr-zoo	*Bruzelia typica*	2.2	SS-Pr-mei	*Bathymedon acutifrons*	4.3
		74.9			68.0			78.7			63.5
BaranaS	**Mar03**			**July03**			**Nov03**			**May04**	
SR-Dt	*Mediterexis mimonectes*	28.6	Ep-Om-mic	*Boreomysis arctica*	36.7	Ep-Om-mic	*Boreomysis arctica*	26.9	Ep-Om-mic	*Boreomysis arctica*	24.5
Ep-Om-mic	*Boreomysis arctica*	16.3	SS-Pr-mei	*Bathymedon longirostris*	11.4	SS-Pr-mei	*Bathymedon acutifrons*	10.9	SS-Pr-mei	*Bathymedon longirostris*	12.7
EP-Pr-zoo	*Eusirus longipes*	4.1	SR-Dt	*Mediterexis mimonectes*	8.1	SS-Pr-mei	*Westwoodilla caecula*	6.4	SS-Pr-mei	*Bathymedon acutifrons*	9.3
SR-Sc-mac	*Tryphosa nana*	4.1	SR-Om-mic	*Munnopsurus atlanticus*	6.7	EP-Pr-zoo	*Rhachotropis caeca*	6.2	EP-Pr-zoo	*Rhachotropis caeca*	6.8
SR-Sc-mac	*Scopelocheirus hopei*	4.1	Ep-Om-mic	*Amblyops trisetosus*	5.5	SR-Om-mic	*Belonectes parvus*	4.2	SR-Om-mic	*Munnopsurus atlanticus*	5.2
SS-Pr-mei	*Bathymedon banyulsensis*	4.1	EP-Pr-zoo	*Rhachotropis caeca*	3.3	SS-Pr-mei	*Bathymedon banyulsensis*	4.0	SR-Dt	*Mediterexis mimonectes*	4.6
		61.2			71.7			58.6			63.1
L3							**Nov03**			**May04**	
						Ep-Om-mic	*Boreomysis arctica*	44.8	Ep-Om-mic	*Boreomysis arctica*	30.0
						SS-Pr-mei	*Oediceropsis brevicornis*	9.7	SR-Sc-mac	*Scopelocheirus hopei*	21.9
						EP-Pr-zoo	*Rhachotropis caeca*	7.6	EP-Pr-zoo	*Rhachotropis caeca*	12.3
						SR-Sc-mac	*Scopelocheirus hopei*	7.0	SR-Om-mic	*Disconectes* sp	7.8
						SS-Pr-mei	*Bathymedon longirostris*	4.0	SR-Dt	*Mediterexis mimonectes*	3.6
						SR-Gr-mic	*Leucon macrorhinus*	3.1	EP-Pr-zoo	*Halice walkeri*	2.6
								76.2			78.2
L5	**Mar03**						**Nov03**			**May04**	
Ep-Om-mic	*Boreomysis arctica*	33.6				SS-Pr-mei	*Bathymedon longirostris*	26.90	Ep-Om-mic	*Boreomysis arctica*	14.8
EP-Pr-zoo	*Rhachotropis caeca*	28.2				EP-Pr-zoo	*Rhachotropis caeca*	23.98	EP-Pr-zoo	*Rhachotropis caeca*	13.5
EP-Pr-zoo	*Rhachotropis glabra*	6.7				Ep-Om-mic	*Boreomysis arctica*	8.19	SS-Pr-mei	*Bathymedon longirostris*	12.5
SS-Pr-mei	*Bathymedon banyulsensis*	4.9				SS-Pr-mei	*Bathymedon banyulsensis*	4.68	SR-Gr-mic	*Diastyloides serratus*	10.8
U	Amphipoda und	4.4				SR-Gr-mic	*Leucon longirostris*	4.68	SR-Gr-mic	*Cyclaspis longicaudata*	4.7
SR-Om-mic	*Belonectes parvus*	3.1				SR-Gr-mic	*Cyclaspis longicaudata*	4.29	SS-Pr-mei	*Bathymedon banyulsensis*	4.4
		80.8						72.7			60.6

Table S2.4.2 Breakdown of percentual contributions from SIMPER analysis for comparisons between water masses (LIW vs.WMDW) and fishing pressure (fished (F) vs.non-fished areas (NF)). The taxa listed contribute at least 0.8%. The six dominant species in each site are marked in bold.

	Density (ind.100m^{-2})					**TG**	**% Contribution (Water masses)**			**% Contribution (Fishing pressure)**		
	Rocassa	Sot	BaranaS	L3	L5		LIW	WMDW	LIW vs. WMDW	F	NF	F vs. NF
	214.5	146.5	49.4	385.3	48.9		AS:50.26	AS:41.52	AD:66.45	AS:41.31	AS:45.84	AD:64.45
Amphipoda												
Eusirus longipes	2.8	2.2	0.6	2.1	0.2	EP-Pr-zoo	2.29	•	•	1.76	•	•
Rhachotropis caeca	3.5	3.9	**2.8**	**41.4**	**9.9**	EP-Pr-zoo	1.79	3.83	1.96	1.86	6.40	2.83
Rhachotropis grimaldii	**11.2**	2.0	0.3	0.6	0.0	EP-Pr-zoo	2.50	-	2.02	1.43	-	•
Rhachotropis rostrata	4.9	1.6	0.7	1.0	0.1	EP-Pr-zoo	2.08	-	•	1.65	•	•
Scopelocheirus hopei	**14.5**	**17.1**	1.1	**65.3**	0.0	SR-Sc-mac	4.35	0.99	3.38	3.14	•	3.31
Bathymedon acutifrons	0.7	**6.1**	**4.2**	4.4	0.9	SS-Pr-mei	1.77	2.21	•	2.14	1.67	•
Bathymedon banyulsensis	0.2	1.3	**1.7**	**7.6**	**2.2**	SS-Pr-mei	•	2.54	•	1.10	2.98	•
Bathymedon longirostris	0.1	0.6	**3.5**	**6.9**	**7.0**	SS-Pr-mei	-	2.77	1.81	•	3.52	2.11
Synchelidium haplocheles	**33.6**	**11.8**	0.2	0.4	0.0	SS-Pr-mei	5.73	•	4.21	2.87	-	2.69
Halice abyssi	1.0	1.6	0.3	2.3	0.7	EP-Pr-zoo	1.45	•	•	1.06	-	•
Mediterexis mimonectes	2.9	1.3	2.3	**9.6**	0.5	SR-Dt	•	2.12	•	1.34	1.09	•
Bruzelia typica	1.6	3.7	0.7	4.8	1.1	EP-Pr-zoo	2.34	1.31	•	1.73	1.64	•
Ileraustroe ilergetes	0.0	0.1	0.5	1.6	1.3	EP-Pr-zoo	-	-	•	-	1.80	•
Syrrhoites cf *pusilla*	0.3	0.2	0.1	1.0	0.8	EP-Pr-zoo	-	•	•	•	1.05	•
Cumacea												
Cyclaspis longicaudata	0.0	0.0	0.4	0.6	**1.7**	SR-Gr-mic		0.99	•	-	1.13	•
Diastyloides serratus	1.5	**4.1**	0.4	6.1	**2.6**	SR-Gr-mic	2.22	0.91	•	1.39	1.56	•
Makrokylindrus longipes	0.1	0.0	0.0	0.8	0.3		-	•	•	-	0.98	•
Leucon longirostris	1.3	3.9	0.6	1.5	1.4	SR-Gr-mic	2.03	1.23	•	1.39	2.05	•
Isopoda												
Belonectes parvus	0.1	0.3	0.9	2.2	0.7	SR-Om-mic	-	1.15	•	•	1.53	•
Munnopsurus atlanticus	**11.6**	**12.5**	**1.7**	4.7	0.2	SR-Om-mic	3.71	0.87	2.29	2.77	•	•
Gnathia sp	7.7	2.2	0.7	4.5	0.2	EP-Sp-fis	2.46	1.29	•	2.13	•	•
Mysida												
Boreomysis arctica	**16.0**	**34.1**	**13.3**	**134.6**	**8.6**	Ep-Om-mic	3.77	6.65	3.60	4.85	6.05	3.96
Hemimysis abyssicola	**76.7**	0.1	0.0	0.0	0	Ep-Om-mic	2.07	-	4.04	0.94	-	2.49
% Contribution of selected taxa:	89.6	75.8	75.3	78.9	83.3							

TG: trophic group; AS: average similarity; AD: average dissimilarity; EP: water column food sources; SR: sediment surface food sources; SS: sediment subsurface food sources; Om: omnivores; Dt: Detritus feeder; Pr: Predator; Sc: Scavenger; Sp: Suctorial parasite, Gr: Grazer; mic: microfauna; mei: meiofauna; mac: macrofauna; zoo: zooplankton; • contribution lower than 0.8%.

Table S2.4.3 Breakdown of percentual contributions from SIMPER analysis for comparisons between fishing grounds (Rocassa, Sot, BaranaS). The taxa listed contribute at least 1.5%. The six dominant species in each site are marked in bold.

	Density (ind.100m^{-2})			**TG**	**% Contribution (Area)**					
	Rocassa 214.5	Sot 146.4	BaranaS 49.4		Rocassa AS: 58.28	Sot AS: 51.32	BaranaS AS: 41.16	Rocassa/Sot AD: 53.15	Rocassa/BaranaS AD: 68.84	Sot/BaranaS AD: 64.17
Amphipoda										
Eusirus longipes	2.8	2.2	0.6	EP-Pr-zoo	2.24	2.25	•	•	•	•
Rhachotropis caeca	3.5	3.9	**2.8**	EP-Pr-zoo	1.49	1.86	1.78	•	•	•
Rhachotropis grimaldii	**11.2**	2	0.3	EP-Pr-zoo	4.55	1.53	•	1.92	3.26	•
Rhachotropis integricauda	4.4	0.1	0	EP-Pr-zoo	2.06	•	-	1.56	2.12	•
Rhachotropis rostrata	4.9	1.6	0.7	EP-Pr-zoo	2.69	1.60	•	•	•	•
Scopelocheirus hopei	**14.5**	**17.1**	1.1	SR-Sc-mac	3.09	5.40	2.38	2.03	2.51	3.86
Bathymedon acutifrons	0.7	**6.1**	**4.2**	SS-Pr-mei	•	2.87	2.91	•	•	1.64
Bathymedon banyulsensis	0.2	1.3	**1.7**	SS-Pr-mei	•	•	2.07	•	•	•
Bathymedon longirostris	0.1	0.6	**3.5**	SS-Pr-mei	•	•	1.51	•	•	•
Synchelidum haplocheles	**33.6**	**11.8**	0.2	SS-Pr-mei	7.17	4.79	•	2.33	5.74	3.58
Westwoodlilla caecula	2	0	1.3	SS-Pr-mei	1.6	-	•	•	•	•
Halice abyssi	1	1.6	0.3	EP-Pr-zoo	•	1.77	•	•	•	•
Mediterexis mimonectes	2.9	1.3	**2.3**	SR-Dt	•	•	4.24	•	•	•
Bruzelia typica	1.6	3.7	0.7	EP-Pr-zoo	1.82	3.11	-	•	•	2.5
Cumacea										
Diastyloides serrata	1.5	4.1	0.4	SR-Gr-mic	1.66	3.02	•	•	•	1.95
Leucon longirostris	1.3	3.9	0.6	SR-Gr-mic	1.66	2.59	•	•	•	1.86
Isopoda										
Munnopsurus atlanticus	**11.6**	**12.5**	1.7	SR-Om-mic	3.98	3.2	1.27	1.55	2.56	2.22
Gnathia sp.	7.7	2.2	0.7	EP-Sp-fis	2.8	2.26	1.93	•	1.85	•
Mysida										
Boreomysis arctica	**16**	**34.1**	**13.3**	EP-Om-mic	3.95	3.15	7.43	3.25	2.04	4.48
Pseudomma affine	0.1	**10.6**	0	Ep-Om-mic	0.0	0.0		•	-	1.66
Hemimysis abyssicola	**76.7**	0.1	0	Ep-Om-mic	8.79	•	-	7.06	8.77	-
% Contribution of selected taxa:	92.5	82.8	80.1							

TG: trophic group; AS: average similarity; AD: average dissimilarity; EP: water column food sources; SR: sediment surface food sources; SS: sediment subsurface food sources; Om: omnivores; Dt: Detritus feeder; Pr: Predator; Sc: Scavenger; Sp: Suctorial parasite, Gr: Grazer; mic: microfauna; mei: meiofauna; mac: macrofauna; zoo: zooplankton; • contribution lower than 1.5%.

2.5 Suprabenthic crustacean assemblages subjected to high-energy hydrodynamic events in the Blanes Canyon and adjacent slope (NW Mediterranean Sea)

Almeida, M., Tecchio, S., Cunha, M.R, Company, J.B. (in preparation). Suprabenthic crustacean assemblages subjected to high-energy hydrodynamic events in the Blanes Canyon and adjacent slope (NW Mediterranean Sea). To be submitted to Journal of Sea Research.

Abstract

Submarine canyons and adjacent slopes from the NW Mediterranean Sea are subjected to high seasonal and inter-annual variability in hydrodynamic processes. Such environmental setting has a profound influence in the spatial and temporal variability of deep-sea benthic assemblages. We analyzed the suprabenthic crustacean assemblages from the Blanes Canyon and adjacent slope along a bathymetric gradient. Hauls were taken from 900 to 2250 m depth in the canyon axis and southwestern adjacent slope in the autumn of 2008, 2009 and 2012. From the twenty four hauls sampled, one hundred and seventy one species were identified. Major changes in densities, number of species and diversity were only found at particular depths or years. In general the samples yielded variable densities (10.1–538.9 ind.100 m^{-2}), mostly owing to temporal fluctuations in motile fauna such as amphipods and mysids, in relation to the occurrence of energy-driven events. The environmental conditions associated to these events coupled with particular topographic features at the shallowest sites (namely at 900 m depth) lead to contrasting biodiversity patterns in the canyon and adjacent slope: high dominance and subsequent depressed diversity in the canyon and the highest diversity on the slope at similar depths. At the deepest sites, suprabenthic diversity reached similar values in the canyon and adjacent slope, probably owing to the decreased influence of disturbance processes at greater depths. Trophic diversity decreased with depth only in the slope, while in the canyon it remained constant likely owing to the relatively enhanced trophic conditions found in the canyon at all depths. However, the community composition differed significantly between the canyon and adjacent slope and at contrasting depths (<1200 m vs.>1200 m). At shallowest depths, the canyon sites were characterized by high motile omnivores while the slope sites were characterized by a high contribution of detritivores. Highly motile predators on zooplankton were dominant at deepest sites in both environments. We suggest that temporal variability in energy driven events, coupled with topographic effects, are the main drivers for the fluctuations in the biodiversity and community structure of deep-sea suprabenthic assemblages in this region.

2.5.1 Introduction

The benthic boundary layer (BBL) plays a crucial role in the exchange of particles between the sediment and the overlying water column; the suprabenthic organisms living in the sediment-water interface are likely to have importance in these processes (Koulouri, 2014). The suprabenthos includes swimming bottom-dependent animals (mainly crustaceans) with migratory behaviour (Brunel et al., 1978) and others with a more temporary relationship with the seafloor (Cartes et al., 2008). This fauna has a recognized relevant role in the benthic-pelagic coupling and deep-sea food webs (Fanelli et al., 2009; Sorbe and Elizalde, 2014). They exploit a large diversity of food resources, mobilizing organic and detritus particles and associated microbes or preying on meiobenthos and plankton, while constituting an important food source for demersal fish and epibenthic crustaceans, including commercial species (Carrassón and Cartes, 2002; Cartes et al., 2008; Madurell et al., 2008; Fanelli et al., 2009). Moreover, the vertical migrations of several species may contribute to the downward fluxes of organic carbon (Dilling and Alldredge, 2000).

The arrival of organic matter to the deep seafloor, primarily from the euphotic zone, but also from lateral advective processes from adjacent shelf and slope areas, is subjected to spatial and temporal variations, mainly due to differences in seafloor morphology and hydrodynamic and atmospheric conditions (e.g. Gooday, 2002; Canals et al., 2006; de Stigter et al., 2007; Smith et al., 2009; Mcclain and Barry, 2010). These variations are particularly relevant in ecosystems characterized by geomorphic features such as submarine canyons. Due to its rough topography, submarine canyons have a complex hydrodynamic regime and are referred to as depocenters, with an important role in channelling particles and sediments from the shelves to the basins (Vetter and Dayton, 1999; Weaver et al., 2004; Harris and Whiteway, 2011), particularly in areas connected to river systems (Puig et al., 2003). The combination of accelerated currents and accumulation of particulate organic matter and nutrient-rich sediments can support high benthic and pelagic faunal densities and biomasses (Macquart-Moulin and Patriti, 1996; Vetter and Dayton, 1999; Ingels et al., 2009; Cunha et al., 2011). The particular conditions of canyons may also modify the faunal assemblage functional spectrum, in comparison with the nearby non-canyon areas at similar depths, by attracting scavengers (e.g. Bernardino et al., 2010), other highly mobile organisms (e.g. Vetter et al., 2010) and suspension-feeders and detritivores (e.g. Vetter and Dayton, 1999). Submarine canyons can also provide recruitment areas for several species, from suprabenthos (Cartes and Sorbe, 1999; Cartes et al., 2010) to fishes and decapods (Sardà et al., 1994; Stefanescu et al., 1994). For all the above reasons, submarine canyons add substantial habitat heterogeneity to continental margins, modifying the common bathymetric patterns of benthic abundance and biodiversity (Rex and Etter, 2010; Cunha et al., 2011). Submarine canyons may enhance mega-epibenthic diversity (Tecchio et al., 2013a) and support distinct communities (Vetter et al., 2010) but decreased macro- and meiobenthic diversity may also occur owing to the high dominance of a few opportunistic species (Cúrdia et al., 2004; Bianchelli et al., 2008; Cunha et al., 2011). However, studies comparing canyons to the adjacent slope also showed limited or no differences in biodiversity, standing stock and feeding types (Bianchelli et al., 2013). In fact, in many studies these comparisons are restricted to a few sites and/or sampling occasions (e.g. Cunha et al., 2011; Romano et al., 2013; Almeida et al., in press) hindering the interpretation of both spatial and temporal patterns. Given the complexity and heterogeneity of submarine canyons, biodiversity patterns cannot be generalized and different benthic compartments and functional groups may exhibit different trends.

The northwestern Mediterranean Sea hosts numerous submarine canyons (Harris and Whiteway, 2011; Canals et al., 2013). Intense investigation in the last decades has shown high seasonal and inter-annual variability in particle fluxes and composition from canyons and open slopes to the deep basins. This variability modulated by the margin´s physiography, is determined by atmospheric and oceanographic processes, regulating primary production (seasonal phytoplanktonic blooms) and the occurrence of high-energy events such as storms and dense-shelf water cascading (Canals et al., 2006, 2013; Zuniga et al., 2009; Sanchez-Vidal et al., 2012; Lopez-Fernandez et al., 2013b). These events occurring from autumn to early spring, mobilize large amounts of organic and inorganic materials and have a great influence on the biodiversity and functioning of Mediterranean margins, canyon systems and deep basins (Company et al., 2008; Pusceddu et al., 2013). In the Mediterranean Sea where low productivity rates and low faunal abundances are reported (Danovaro et al., 1999; Tselepides et al., 2000), such environmental setting is of special relevance to interpret the spatial and temporal variability of deep-sea biological assemblages. This study examines the abundance, biodiversity and trophic structure of suprabenthic crustacean assemblages in the Blanes Canyon area along a bathymetric gradient from 2008 to 2012. We aim to i) compare the abundance, suprabenthic structure and biodiversity in the Blanes canyon and the adjacent slope ii) discuss patterns in abundance and biodiversity of the suprabenthic assemblages in relation to spatial and inter-annual changes in environmental conditions (e.g. current flow, particle fluxes).

2.5.2 Material and methods

2.5.2.1 Study area

Circulation in the northwestern Mediterranean Sea is characterized by the interaction of three major water masses: the Atlantic Water (AW, 15-20°C; salinity: 36-36.5 psu) originates from surface inflows in the Strait of Gibraltar and extends from the surface to 100-200 m depth (Millot, 1999); the Levantine Intermediate Water (LIW), a salty and warm water mass (14ºC and 38.75 psu), originates in the eastern Mediterranean basin around 300-400 m and extends down approx. 600 m; below this depth, lies the Western Mediterranean Deep Water (WMDW, 13°C and 39 psu), formed in the Gulf of Lion by deep-ocean convection (Font et al., 1995; Millot, 1999).

The Catalan Sea is incised by three main canyons, from North to South, Cap the Creus, La Fonera, and Blanes canyons. The target of this study, the Blanes Canyon, starts around 60 m deep at less than 4 km off the coastline; it is 184 km long and displays a nearly N–S trending upper course incising down to 1500 m into the continental shelf (Amblas et al., 2006). The width of the canyon increases with depth up to 20 km and ends at 2400 m depths in the Valencia channel. The canyon has a V-shaped cross section in the upper course and a U-shaped cross section in the middle and lower courses indicating the prevalence of erosion and accumulation processes, respectively (Lastras et al., 2011). The canyon walls show contrasting morphologies which affect the near-bottom currents, with a high variable flow in the smoother eastern wall and a unidirectional offshore flow over the western wall (Zuniga et al., 2009).

High concentrations of near-bottom particle fluxes (average Total mass flux, TMF) reported from the adjacent slope at 900-1200 m depths in 2009 were likely caused by lateral advection from the nearby gullies carved in Blanes Canyon flanks (Lopez-Fernandez et al., 2013b). The high amount of particles transported down the canyon, in general one order of magnitude higher than in the adjacent slope (TMF: 18.35 and 1.88 $gm^{-2}d^{-1}$, respectively), can be explained by the relatively large sediment drainage area opening into the canyon, the incision length of the canyon into the shelf, the closeness of its head to the shoreline and the proximity of the Tordera River (Zuniga et al., 2009; Durán et al., 2013). Increasing TMF values were observed down the canyon axis from 300 to 1500 m (300 m: 12.68 $gm^{-2}d^{-1}$; 900 m: 15.39 $gm^{-2}d^{-1}$, 1200 m: 23.82 $gm^{-2}d^{-1}$, 1500 m: 26.57 $gm^{-2}d^{-1}$), illustrating the step-by-step transport along the canyon involving the resuspension of particles previously accumulated in its shallower reaches (Lopez-Fernandez et al., 2013b).

Lopez-Fernandez et al. (2013b) also reported a noticeable temporal variability of TMF along the canyon axis during 2008 and 2009: in December 2008 maximum values were observed at 900, 1200 and 1500 m (up to 35.29, 75.38 and 50.03 gm^{-2}d^{-1}, respectively). TMF peaked again during 2009 but in July at 900 m (25.15 gm^{-2}d^{-1}), in March at 1200 m (42.21 gm^{-2}d^{-1}) and in February at 1500 m (51.19 gm^{-2}d^{-}1). High seasonal and inter-annual variability in the flux of particles in the Blanes Canyon is determined mostly by offshore convection and by the occurrence of oceanic storms, dense shelf-water cascading episodes (DSWC), and phytoplankton blooms (Zuniga et al., 2009; Lopez-Fernandez et al., 2013b). Resuspension by trawling disturbance and dust inputs are additional sources of particles affecting the flux variability (Lopez-Fernandez et al., 2013b).

In the winter and spring of 2009 oceanic storms, including the most extreme storm measured in the area in November 2008-January 2009 (Sanchez-Vidal et al., 2012), triggered high waves and intensified currents resuspending and remobilising sediment over the continental shelf down to unusually great water depths. Significant current increases associated to this major storm were observed along the canyon axis (300 m: up to 70 cm s^{-1}; 900 m: up to 27 cm s^{-1}; 1200 m: 32 cm s^{-1}; 1500 m: 25 cm s^{-1}) and were also noticeable, to a less extent, in the adjacent slope. The January and April 2009 moderate storms affected only the canyon down to 1200 m (900 m: 19-23 cm.s^{-1}; 1200 m: 27-28 cm.s^{-1}). During the period between November 2008 and November 2009, the annual mean current speed in the canyon decreased gradually from 7.7 to 6.7 cm.s^{-1} with increasing water depths from 300 to 1200 m, and then more markedly reaching 4.2 cm.s^{-1} at 1500 m.

The winter of 2012 experienced peculiar atmospheric conditions that lead to the formation of a DSWC in the region (Durrieu de Madron et al., 2013). In years of intense DSWC (e.g. 1998-1999, 2004-2005, 2011-2012) water cascades down to more than 2000 m, with velocities close to 1 m.s^{-1} measured in the submarine canyons seafloor (Canals et al., 2006; Durrieu de Madron et al., 2013, Sanchez-Vidal et al., 2015).

2.5.2.2 Sample collection and processing

Four oceanographic cruises were performed in the Blanes Canyon (BC) and adjacent slope (OS) in October 2008 (Prometeo I cruise), September and November 2009

(Prometeo IV and V cruises, respectively) and October 2012 (DOSMARES III cruise) on board the R/V García del Cid, along a bathymetric gradient ranging from 900 to 2250 m: i) during Prometeo I cruise two sites were sampled in the adjacent slope at 900 and 1500 m; ii) during Prometeo IV and V cruises (Sept and Nov 2009) samples were collected along a bathymetric gradient from 900 to 1750 m in the adjacent slope and in addition, two samples were taken at 900 and 1500 m in the Blanes Canyon; iii) during DOSMARES III, samples were collected at 1500, 2000 and 2250 m depth in the Blanes Canyon and adjacent slope; an additional sampling was obtained at 1200 m inside the canyon (Fig. 2.5.1). In total, sixteen hauls from the southwest adjacent slope and eight hauls from the canyon axis were analysed in the present study (metadata shown in Table 2.5.1). The suprabenthos sampling effort was not consistent between years, as samples were unevenly distributed between the canyon and the adjacent slope.

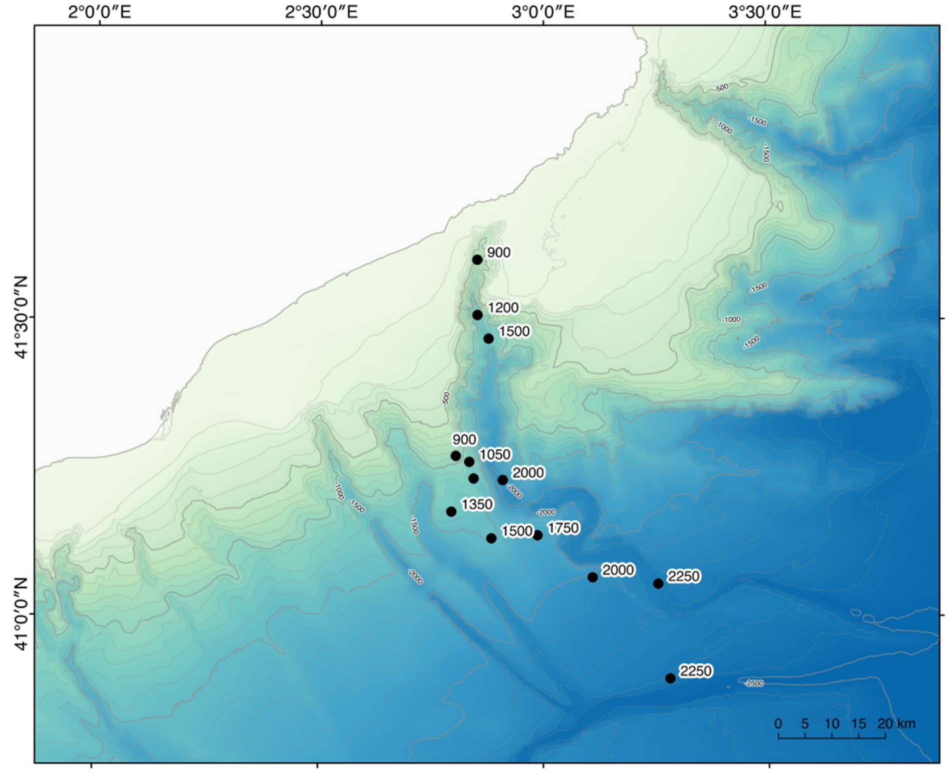

Figure 2.5.1 Location of the study sites (dots) in the Blanes Canyon area, Western Mediterranean Sea.

Table 2.5.1 Metadata of the sledge hauls taken in the Blanes Canyon area. OS: adjacent slope; BC: Blanes Canyon.

Code	Date (d/m/y)	Topography	Mean depth (m)	Hour[a] (h:m)	Position[a] Latitude (N)	Longitude (E)	Length[b] (m)
PR1P01	27/10/08	OS	900	12:35	41°15.41'	2°48.25'	1234.7
PR1P05	28/10/08	OS	1520	02:09	41°07.18'	2°52.39'	1566.5
PR4P2	05/09/09	OS	1200	14:24	41°14.00'	2°49.99'	1055.6
PR4P3	05/09/09	OS	900	16:12	41°15.77'	2°48.16'	2389.1
PR4P4	11/09/09	BC	900	15:36	41°35.67'	2°51.06'	2284.1
PR4P10	12/09/09	OS	900	07:57	41°15.71'	2°47.91'	2531.1
PR4P9	12/09/09	OS	1050	05:56	41°15.41'	2°49.64'	2531.1
PR4P8	12/09/09	OS	1200	03:47	41°13.92'	2°49.96'	2592.8
PR4P7	12/09/09	OS	1350	01:22	41°09.99'	2°47.41'	2345.9
PR4P5	11/09/09	BC	1500	18:01	41°28.30'	2°52.18'	3086.7
PR4P6	11/09/09	OS	1500	22:29	41°07.47'	2°52.18'	1481.6
BF2P7	03/11/09	BC	900	00:11	41°35.14'	2°50.92'	1852.0
BF2P9	04/11/09	OS	1200	11:31	41°14.33'	2°50.10'	1852.0
BF2P3	01/11/09	OS	1500	14:30	41°07.58'	2°52.62'	1790.3
BF2P5	02/11/09	BC	1500	20:20	41°27.70'	2°52.38'	3086.7
BF2P2	30/10/09	OS	1750	18:55	41°08.17'	2°58.72'	2469.3
BF2P1	30/10/09	OS	2000	15:26	41°02.76'	3°03.27'	2037.2
DM2P11	10/10/12	BC	1200	22:44	41°30.33'	2°51.08'	1731.6
DM2P3	09/10/12	OS	1500	15:06	41°07.23'	2°50.22'	2024.9
DM2P10	10/10/12	BC	1500	19:37	41°26.11'	2°53.11'	1521.7
DM2P5	09/10/12	OS	2000	21:37	41°04.02'	3°06.33'	2963.2
DM2P8	10/10/12	BC	2000	11:47	41°13.51'	2°54.33'	2864.4
DM2P6	10/10/12	OS	2250	02:00	40°56.49'	3°16.52'	2963.2
DM2P7	10/10/12	BC	2250	06:48	41°03.23'	3°15.18'	2963.2

a) beginning of the haul; b) linear distance sampled by the sledge during the haul.

At each site, suprabenthos was collected with a modified version of the Macer-GIROQ sledge (see Cartes et al., 1994 for a full description). This gear, equipped with three superimposed nets (0.5 mm mesh size; 80 cm width and 40 cm height), quantitatively samples the fauna in three water layers above the bottom (10-45 cm, 50-95 cm and 100-140 cm). The sledge was hauled at approx. 2 knots around 30-60 min. Due to time-consuming sampling during the descent of the sled and towing over the seafloor, no replicates could be performed (except in PROMETEO IV cruise in the slope at 900 and 1200 m, with two hauls each). However, the replicability of a similar gear at shelf and slope depths was tested by Brattegard and Fossa (1991) who concluded that, in a cost-efficient context, one sample is representative of a site. The fauna collected was sieved with a mesh size 0.5 mm and fixed in 10% neutral formalin on board. In the lab, samples were stored in 70% ethanol and sorted to major taxa. Crustaceans, except Copepoda and Ostracoda (considered as meiofauna), were identified at species level whenever possible and counted. The remaining fauna, i.e. endobenthic groups (e.g. polychaetes, bivalves, ophiuroids), pelagic groups (e.g. chaetognaths, tunicates) and larvae were excluded from the analysis. The swept area (A) was calculated with the following formula: A= SxBTxWx1852 (S: mean haul speed in knots; BT: bottom time in decimal hours; W: width of net opening; 1852 is the conversion factor from nautical miles to meters; SxBT corresponds to the estimate of the distance travelled during seafloor sampling). The densities of each taxa were expressed as number of individuals per 100 m^2 for the 10-140 cm water layer (total fauna).

2.5.2.3 Data analysis

The abundance data was used to calculate taxonomic and trophic biodiversity: number of species (S) and trophic guilds (TG), Shannon-Wiener diversity index (H'), Pielou (1969) evenness index (J') and Hurlbert's expected number of species and trophic guilds, $ES_{(n)}$ and $ETG_{(n)}$ (Hurlbert, 1971), respectively. The abundance data (expressed as ind.100 m^{-2}) was analyzed by means of non-metric multidimensional scaling (MDS) ordination, using the Bray-Curtis similarity measure, after square root transformation of the data. An analysis of similarities by randomization/permutation tests (ANOSIM) was performed to assess the significance of differences in the suprabenthic assemblages putatively related to location (slope vs. canyon) and depth (<1200 m vs. >1200 m). As mentioned above, the depth strata of 1200 m was recently highlighted as a zone of accumulation of nutrients, being hypothesized that it could represent an ecotone-like boundary (Tecchio et al., 2013a). SIMPER analysis (Similarity Percentages – species contributions) was applied to determine the percentage contributions of each species to the similarity within and dissimilarity between groups of samples. The species were also ranked by decreasing abundance to illustrate spatial and temporal changes in dominance. Diversity measures and multivariate analyses were performed using the PRIMER software package (Clarke and Gorley, 2006).

To assess the trophic structure, a trophic guild was allocated to each taxa based on food source, food type and size and feeding mode (adapted from Macdonald et al., 2010 with information compiled from Cartes 1998a; Madurell et al., 2008, Fanelli et al., 2009). Food source (or foraging behaviour) of suprabenthic assemblages was classified into three categories: water column/epibenthic (EP), seafloor surface (SR) and sediment subsurface (SS). The categories for food type and size were sediment (sed), particulate organic matter (pom), microfauna (mic), meiofauna (mei), macrofauna (mac), phytodetritus (phy), zooplankton (zoo) and fish (fis). Feeding mode was assigned as detritus feeder (Dt), suspension/filter feeder (Su), predator (Pr), scavenger (Sc), suctorial parasite (Sp), grazer (Gr) and omnivore (Om) (for more details see MacDonald et al., 2010).

To analyse inter-annual changes in the suprabenthic assemblage composition the turnover (or species replacement) across months and years was assessed for the sites sampled in two or more consecutive sampling occasions (e.g. Magurran, 2004). The index used was T= (L+G)/S; where L is the number of taxa lost, G is the number of taxa gained and S is the pooled number of taxa in the two consecutive months or years; T values vary between 0 (no changes in the assemblage; G=0 and L=0) and 1 (complete renovation of the assemblage; L+G=S).

2.5.3 Results

A total of 49726 specimens collected from the 24 hauls were ascribed to 171 taxa (Table 2.5.2 and Figs. 2.5.2-2.5.3). In general, the fauna was concentrated in the near-bottom water layer (approximately 70% of total haul abundance at 10-50 cm), and decreased in the upper water layers (55-95 cm and 100-140 cm). The data presented here integrate the results obtained from the three water layers. Amphipods were the most speciose and abundant group (65 species; 39.2% of total abundance). Mysids were the second most abundant (35.8%) group but represented by considerably fewer species (12). Cumaceans, isopods and decapods presented intermediate numbers of species (36, 24 and 23, respectively) but much lower values of abundance (9.5, 7.1 and 1.2%, respectively) and euphausiids (6 species; 6.9%) were less common. Other groups (Lophogastrida, Tanaidacea and Leptostraca) were represented in the samples by only a few individuals (total of 5 species; <1.0% of total abundance). Estimated densities were the highest at BC900 (435.7 and 538.9 ind.100 m^{-2} in Sept and Nov 2009, respectively) and showed typically low values (<50 ind.100 m^{-2}) in OS sites during 2009 (Fig. 2.5.2). The number of species per sample varied between 31 (BC1500, Nov 2009, note that the sampled area was rather small) and 84 (OS2000 and BC2000, Oct 2012).

The suprabenthic assemblages showed a wide spectrum of trophic guilds (16 categories, Table 2.5.2 and Fig. 2.5.4). Predators on zooplankton (Eusiridae and Synopiidae amphipods: EP-Pr-zoo) were the most represented group followed by predators on meiobenthos (Oedicerotidae amphipods: SR-Pr-mei; Nannastacidae cumaceans: SS-Pr-mei) omnivores (mysids: EP-Om-mic; Munnopsidae isopods: SR-Om-mic) and microbial grazers (Diastylidae and Leuconidae cumaceans: SR-Gr-mic) that were also well-represented groups.

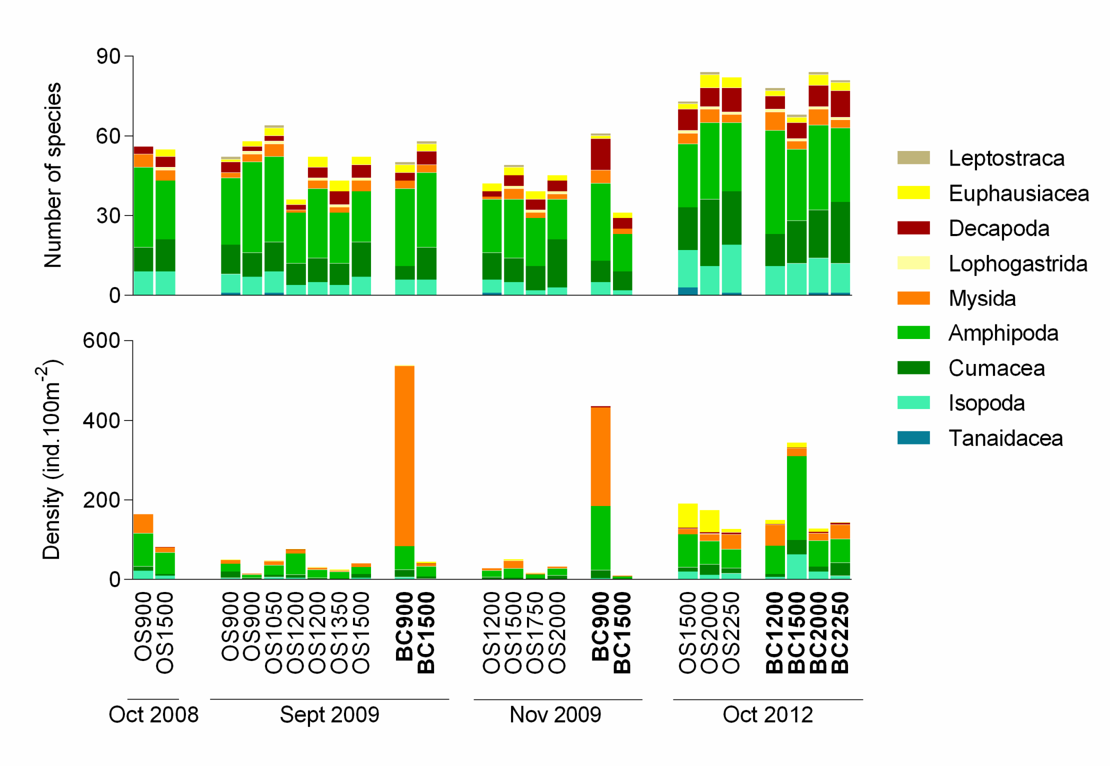

Figure 2.5.2 Number of species and density (ind. 100 m^{-2}) of suprabenthic fauna collected throughout the sampling period (2008, 2009 and 2012) in the Blanes Canyon and adjacent slope. OS: slope sites; BC: Blanes Canyon sites; Oct 2008: samples collected in October 2008; Sept 2009: samples collected in September 2009: Nov 09: samples collected in November 2009; Oct 2012: samples collected in October 2012.

Table 2.5.2 Density (D), abundance (A), biodiversity and trophic data of the suprabenthic samples. S: number of species; TG: number of trophic guilds; H’: Shannon-Wiener diversity index; J′- Pielou's evenness; $ES_{(100)}$ and $ETG_{(100)}$ – Hurlbert's expected number of species and trophic guilds per 100 individuals, respectively; OS: slope sites; BC: Blanes Canyon sites.

Time	**Site**	**D**	**A**	**Taxonomic diversity**				**Trophic diversity**			
		(ind 100 m^{-2})		**S**	**H'**	**J'**	**$ES_{(100)}$**	**TG**	**H'**	**J'**	**$ETG_{(100)}$**
Oct2008											
	OS900	165.1	1631	56	2.93	0.728	25.5	13	1.91	0.746	8.9
	OS1500	82.5	1034	55	2.64	0.659	22.3	14	1.52	0.575	8.1
Sept2009											
	OS900	49.9	953	52	2.7	0.683	23.4	14	1.94	0.737	9.8
	OS900	16.1	325	58	3.35	0.826	35.3	14	2.08	0.79	11.6
	OS1050	48	972	64	3.07	0.739	28.4	13	1.96	0.764	9.7
	OS1200	76.5	646	36	2.78	0.777	22.3	12	1.6	0.645	7.9
	OS1200	31.4	652	52	3.04	0.77	28.2	13	1.73	0.676	9.8
	OS1350	25.6	481	43	2.98	0.791	26.3	13	1.54	0.602	8.5
	OS1500	42.4	502	52	3.01	0.762	27.1	13	1.74	0.68	8.9
	BC900	538.9	9848	50	1.28	0.328	9.9	12	0.68	0.275	5.8
	BC1500	44.7	1103	58	3.06	0.754	26.4	15	1.73	0.64	10.3
nov/09											
	OS1200	29.7	440	42	2.43	0.65	22.1	13	1.66	0.646	9
	OS1500	50.6	725	49	2.57	0.661	23	13	1.4	0.546	8.2
	OS1750	16.9	333	39	3	0.819	26.9	13	1.68	0.656	10.2
	OS2000	33.6	548	45	2.97	0.779	25.3	12	1.67	0.671	8.8
	BC900	435.7	6456	61	1.83	0.445	12.7	15	1.07	0.393	5.9
	BC1500	10.1	250	31	2.79	0.812	22.8	12	1.72	0.691	9.4
Oct2012											
	OS1500	190.4	3084	73	2.57	0.599	22.5	16	1.26	0.453	8.3
	OS2000	173.8	4121	84	2.81	0.635	26.3	14	1.47	0.558	8.7
	OS2250	127.4	3021	82	3.04	0.69	29.4	14	1.79	0.68	9.4
	BC1200	149.1	2066	78	2.74	0.629	24.5	16	1.65	0.594	9.1
	BC1500	344.6	4195	68	2.51	0.595	21.8	16	1.35	0.489	7
	BC2000	128.2	2938	84	2.84	0.641	25.5	15	1.63	0.603	9
	BC2250	143.5	3402	81	2.9	0.661	26.5	15	1.8	0.664	9.1
OS				145			31.2	16			9.9
BC				144			25.1	16			8.5

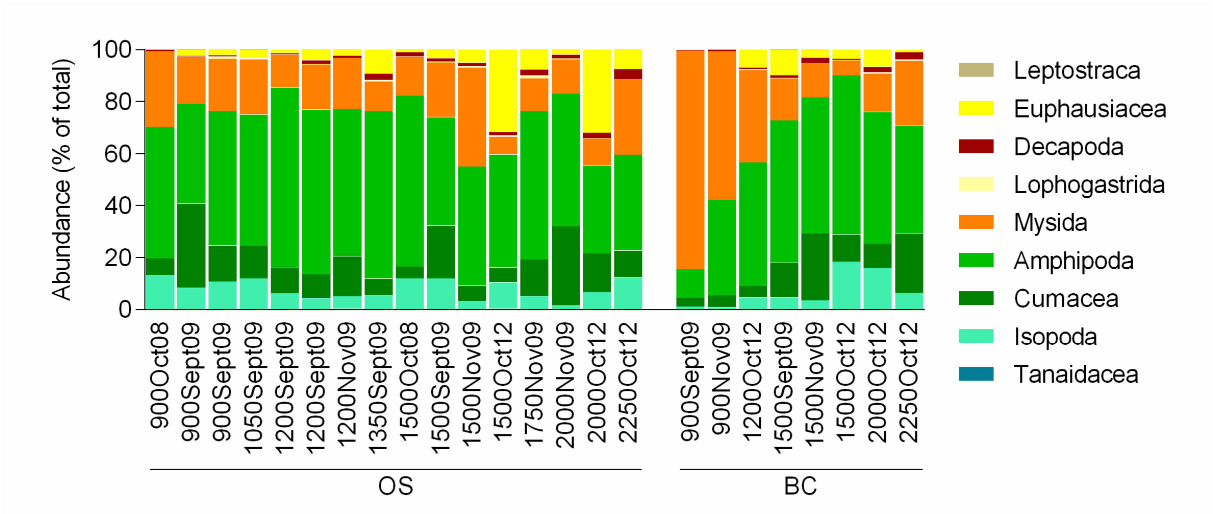

Figure 2.5.3 Relative abundance of the main taxonomic groups of suprabenthic fauna collected throughout the sampling period (2008, 2009 and 2012) the Blanes Canyon and adjacent slope. OS: slope sites; BC: Blanes Canyon sites; Oct 2008: samples collected in October 2008; Sept 2009: samples collected in September 2009: Nov 09: samples collected in November 2009; Oct 2012: samples collected in October 2012.

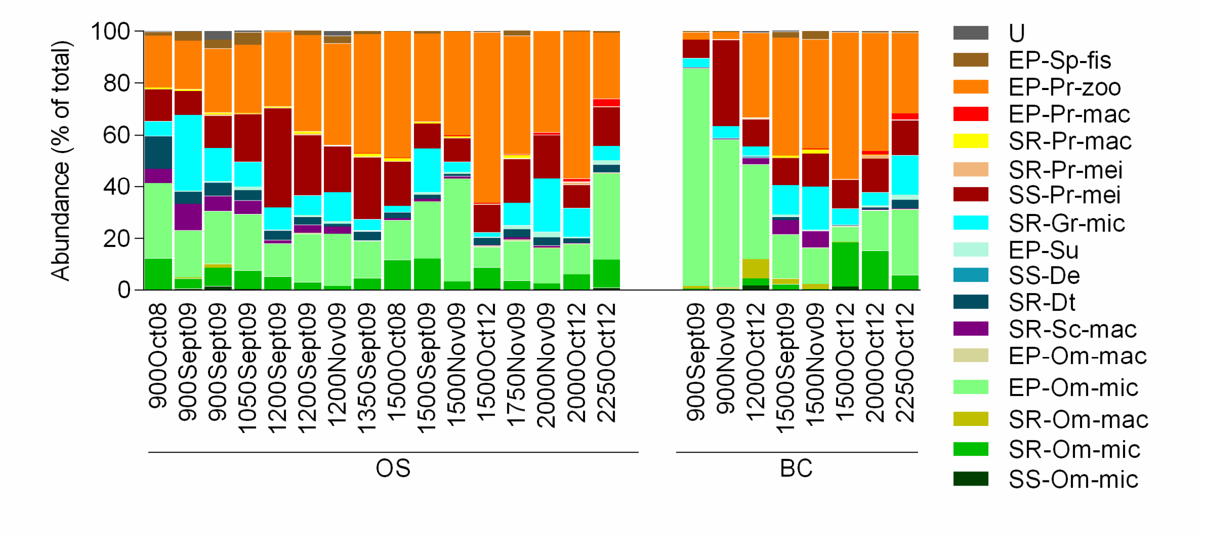

Figure 2.5.4 Relative abundance of the trophic groups of suprabenthic fauna collected throughout the sampling period (2008, 2009 and 2012) the Blanes Canyon and adjacent slope. OS: slope sites; BC: Blanes Canyon sites; Oct 2008: samples collected in October 2008; Sept 2009: samples collected in September 2009: Nov 09: samples collected in November 2009; Oct 2012: samples collected in October 2012.

2.5.3.1 Temporal fluctuactions in the suprabenthic assemblages

Overall and for comparable depths, the suprabenthic crustacean assemblage showed higher abundance, number of species and number of trophic groups but lower evenness in 2012 (Table 2.5.2, Figs. 2.5.2-2.5.3; note that BC900 was not sampled in 2012). In all sites that could be directly comparable (OS1500, OS2000 and BC1500; Table 2.5.2) densities increased 3-5 fold, the number of species almost doubled (more than doubled at BC1500) and the number of trophic guilds increased from 12-13 to 14-16. Euphausiids, that were much less abundant in 2008 and 2009, contributed considerably to the enhanced densities at OS1500 and OS2000 in 2012. The numbers of decapod, isopod and cumacean species (mostly predators on macrofauna, surface omnnivores and microbial grazers) were also noticeably increased in 2012 (Fig. 2.5.2).

Temporal changes in the composition of suprabenthic assemblages are best revealed by analysing the sites which were sampled in various occasions (namely at 1500 m). Similar turnover values were obtained when analysing the species replacement at the slope at 900 m (Sept2009 to Nov2009), 1200 m (Sept2009 to Nov2009) and 1500 m depth (Oct2008 to Sept2009, Sept2009 to Nov2009 and Nov2009 to Oct2012). Here, the turnover values ranged 45-49% at all temporal scales. In the BC at 900 m turnover values from Sept2009 to Nov09 were slightly higher (52%) but a more dynamic pattern was revealed at 1500 m where turnover reached values of 63% (Sept2009 to Nov2009) and 78% (Nov2009-Oct2012). These values were determined mostly by losses in the number of species from Sept2009 to Nov2009 (34 species) and gain of species from Nov2009 to Oct2012 (47 species).

2.5.3.2 Canyon vs. adjacent slope

The canyon and adjacent slope assemblages showed similar pooled numbers of species (144 and 145, respectively from which 118 were common to both environments) representing the same trophic groups (16). The sampling effort was lower in the canyon than in the adjacent slope (8 and 15 hauls, respectively) but rarefied biodiversity indices of the pooled assemblages (Table 2.5.2) show higher values in OS ($ES_{(100)}$ 31.2; $ETG_{(100)}$ 9.9) than in BC ($ES_{(100)}$ 25.1; $ETG_{(100)}$ 8.5). The rarefaction curves plotted for every haul (Fig. 2.5.5) also indicate generally higher (alpha-) diversity in the slope than in the canyon.

Differences in densities were observed between the canyon and adjacent slope. Maximum densities were observed at shallower sites in the BC due to the high contributions of mysids (248.5 and 452.7 ind.100 m^{-2} in site BC900 in Sept 09 and Nov09, respectively; Fig. 2.5.2 and 2.5.4). In fact, the highest number of mysid species was also observed in the BC (e.g. 7 species in the site BC1200 in contrast with only one species in the sites OS1200 in Sept09 and Nov09). In 2012, a peak in densities was observed in BC but at 1500 m depth and owing to an increased contribution of amphipods, isopods and, to a less extent, also cumaceans. These density peaks were associated to the high dominance (Table 2.5.2) in the canyon assemblages. At BC1500, the dominant species were a predator on zooplankton, the amphipod *Rhachotropis glabra* (38.0%), and the surface omnivore isopod *Belonectes parvus* (12.3%) (Supplementary material, Table S2.5.1). At BC900 m, the epibenthic ominivore mysid *H. abyssicola* (42.2-64.8%) and a predator on meiobenthos, the amphipod *Synchelidium haplocheles* (5.3-22.3%), reached their highest dominance (Supplementary material, Table S2.5.1) leading to the lowest rarefaction curves (Fig. 2.5.5), taxonomic and trophic diversity and evenness values observed during the study ($ES_{(100)}<13$; $J'<0.45$; $ETG_{(100)}<6$ $J'_{TG}<0.40$; Table 2.5.2). Contrastingly the highest values of these indices were observed at the same depth but in OS ($ES_{(100)}$: 35.3; J': 0.826; $ETG_{(100)}$: 11.6 J'_{TG}: 0.790, in Sep09; Table 2.5.2, Fig. 2.5.6B) where the dominant ranks were more evenly shared by a taxonomically and trophically diverse array of species such as the epibenthic omnivore mysid *Boreomysis arctica*, the surface grazer cumacean *Leucon longirostris*, the surface detritivore amphipod *Mediterexis mimonectes*, and a predator on zooplankton, the amphipod *Rhachotropis caeca* (Supplementary material, Table S2.5.1).

Overall, the canyon and adjacent slope assemblages showed differences in their taxonomic and trophic structure (Fig. 2.5.3 and 2.5.4). In the slope, the relative abundance of the highly motile component of suprabenthos (mysids, lophogastriids, euphausiids and decapods) increased with depth (14.6% in the site OS1200 in Sept09 to 44.7% OS2000 in Oct12). This was especially evident in 2012 when euphausiids (*Nematoscelis megalops*) attained their highest relative abundance (31.7%) at OS2000. In the canyon, the inverse trend was observed with a decrease in the relative abundance of the highly motile component of suprabenthos with increasing depth from a maximum of 84.4% (BC900 in Sep09) to a minimum of 9.9% (BC1500, Oct 2012) (Fig. 2.5.3). Epibenthic predators on zooplankton tended to be the dominant trophic group in the studied suprabenthic assemblages but in BC they were replaced by epibenthic omnivores (mostly mysids) at the shallower depths where trophic evenness reached its minimum (<0.4 at BC900; Table

2.5.2) while in OS at the similar depths trophic evenness showed typically higher values (>0.6; Table 2.5.2). OS assemblages showed also more regular contributions of trophic groups feeding in association with the sediments, such as predators on meiofauna (e.g. *Bathymedon longirostris*) and detritivores (eg. *M. mimonectes*) (Fig. 2.5.4).

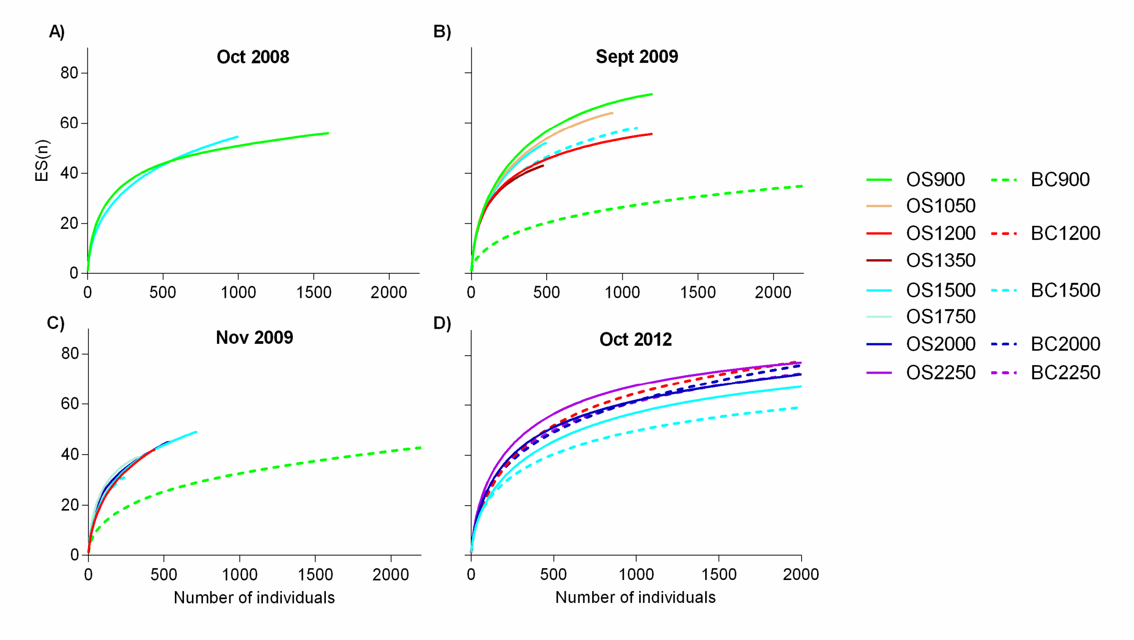

Figure 2.5.5 Rarefaction curves for the four sampling periods. A) October 2008; B) September 2009; C) November 2009; D) October 2012. Full line: slope sites; Dashed line: Blanes Canyon sites.

2.5.3.3 Depth-related changes

No clear depth-related trends were observed, except for the overall increase in densities and species richness at the deepest sites in 2012. Figure 2.5.6 shows that both taxonomic and trophic rarefied diversity show typically similar values and comparable variability within and between depths ($ES_{(100)}$: 21.8-29.4; $ETG_{(100)}$: 7.0-10.2). The exception is the shallowest sites (900 m) where different trends were observed for the canyon (lower values, $ES_{(100)}$: 9.9-12.7; $ETG_{(100)}$: 5.8-5.9) and the adjacent slope (higher values, $ES_{(100)}$: 23.4-35.3; $ETG_{(100)}$: 8.9-11.6) as already mentioned above (section 2.5.3.2).

More clear changes were observed in the composition and trophic structure of the assemblages. The relative contribution of predators on zooplankton generally increased with depth (maximum relative contribution: 56.6% at BC1500 and 65.9% at OS1500 in Oct12). Despite their low abundances, in general scavengers (SR-Sc-mac; SR-Om-mac) occurred only at shallowest sites.

Important shifts in the dominant species were observed along the depth gradient. In general, the eusirids *Rhachotropis caeca* (5.4-32.5%) and *R. glabra* (4.8-13.0%), the oedicerotid *Bathymedon longirostris* (5.7-38.0%) and the mysid *Boreomysis arctica* (3.6-34.3%) were dominant species across all the bathymetric range an in both environments. The cumacean *Leucon longirostris* (3.6-22.8%) and the amphipod *Mediterexis mimonectes* (4.5-12.4%) were abundant species shallower than 1200 m, while deeper that 1200 m the amphipod *Ileraustroe ilergetes* (3.2-14.0%) and the euphausiid *Nematoscelis megalops* (3.2-30.8%) were numerically abundant. The isopod *Belonectes parvus* (4.4-12.4%) and several cumacean species were numerically abundant deeper than 1500 m (Supplementary Material, Table S2.5.1).

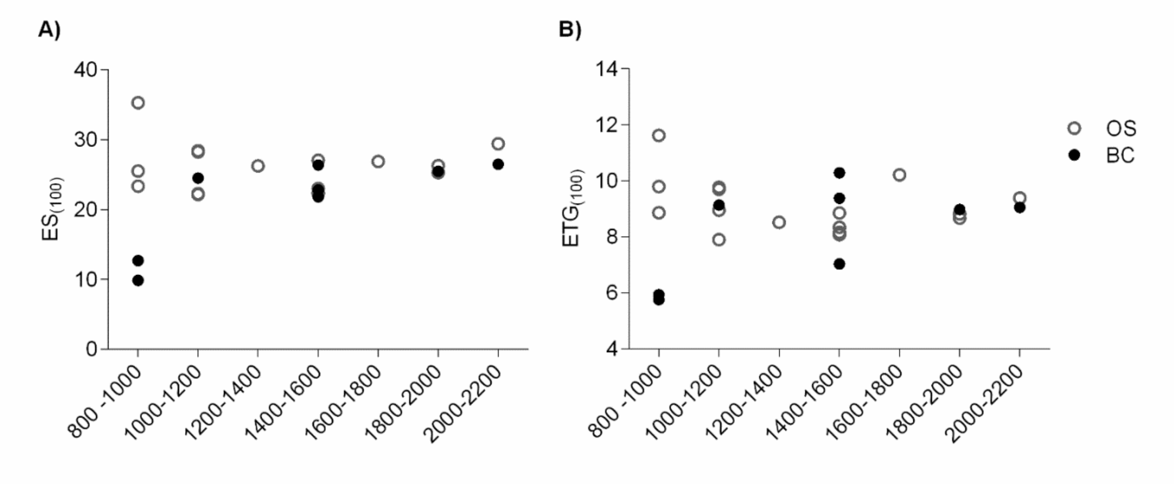

Figure 2.5.6 Expected number of species (A) and trophic guilds (B) for 100 individuals in all sites. OS: slope sites; BC: Blanes Canyon sites.

More clear trends in diversity are observed when considering the highly motile taxa (mysids, lophogastriids, euphausiids and decapods) and the less motile taxa (amphipods, isopods, cumaceans and tanaids) separately (Figure 2.5.7). The expected number of species for the assemblage with more affinity to the bottom (less motile) suggests an inversed hump-shaped curve in the adjacent slope and an increase in diversity with depth in the canyon (Fig. 2.5.7A), whereas for the high motile component of suprabenthos a hump-shaped pattern is observed for both assemblages. Note that this interpretation may be biased by the fact that most deep sites were sampled only in 2012 and therefore there is a probable interaction between depth and time of sampling.

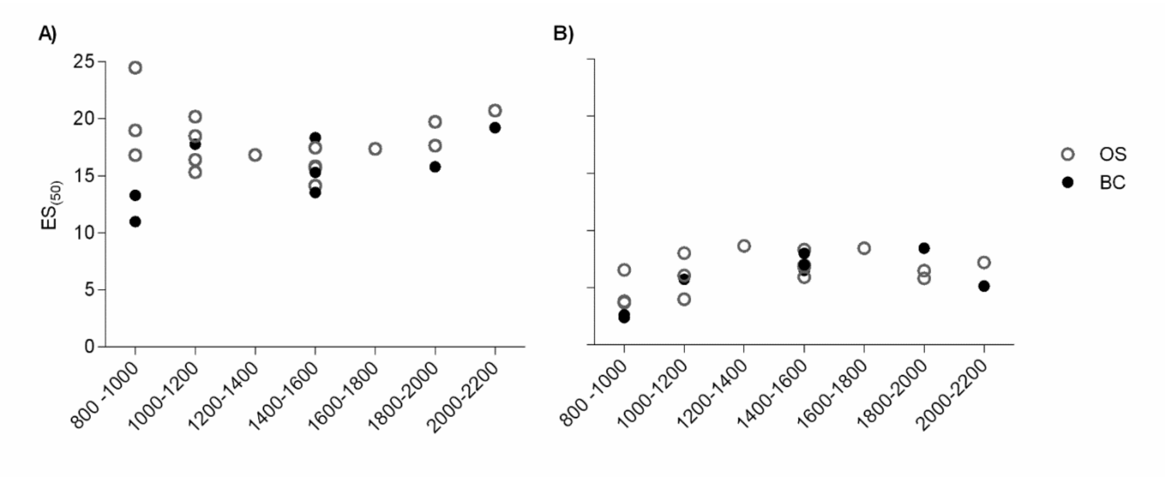

Figure 2.5.7 Expected number of species (n: 50 individuals) for less motile (A) and highly motile fauna (B) in all sites. OS: slope sites; BC: Blanes C anyon sites.

2.5.3.4 Multivariate analysis

Multivariate analysis was used to asses for the significance of spatial patterns in the suprabenthic crustacean assemblages. Two factors were considered: location (BC vs.OS) and depth (<1200 m vs.>1200 m). The MDS plot (Fig. 2.5.8) shows a clear segregation of the samples by the two depth categories while the separation between OS and BC is less clear with the OS samples aggregated in the centre of the plot and the BC samples more dispersed over various quadrants. The samples from 2012 also tended to aggregate (bottom of the plot). Because the sampling over the three years was not consistent in terms of areas and depths sampled, the time factor could not be adequately tested by the ANOSIM routine. Therefore the interpretation of the spatial patterns must take into account the possible interaction with the “time” factor. The effects of both “location” (ANOSIM, R=0.460, P=0.06%) and “depth” (R=0.434, P=0.04%) were significant (Table 2.5.3). The average similarity within groups and the dissimilarity between groups (Table

2.5.4) showed similar and relatively low values (45-57%) for the factor “depth” (across “location” groups) and “location” (across “depth” groups).

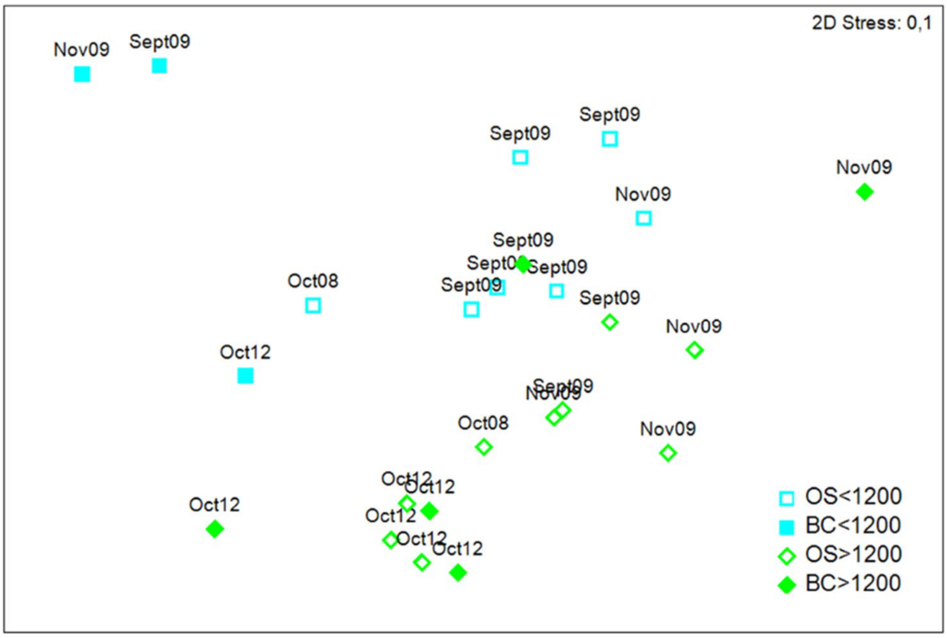

Figure 2.5.8 MDS plot of the suprabenthic crustacean assemblages from the Blanes canyon and adjacent slope. Oct08: October 2008; Sept09: September 2009; Nov09: November 2009; Oct12: October 2012. <1200: samples collected at 1200 m depth or shallower; >1200: samples collected at depths greater than 1200 m. Open symbols: slope samples; Full symbols: canyon samples.

Table 2.5.3 Results of the ANOSIM two-way crossed analysis with the factors “depth” (<1200 m, >1200 m) and “location” (canyon and adjacent slope).

	Sample Statistic	Permutations used	Significant statistics	P (%)	
Global test					
Location	0.460	9999	5	0.06	**
Depth	0.434	9999	3	0.04	**

**Very Significant

The dominant species were generally retrieved by the SIMPER analysis as the major contributors for the similarity and dissimilarity of the groups of samples. Three species were dominant across both locations and depths: the mysid *Boreomysis artica* (EP-Om-mic) and the amphipods *Rhachotropis caeca* and *R. glabra* (EP-Pr-zoo). These species were relevant not only by their contributions to the similarity within groups because of their constant occurrence but also to the dissimilarity between groups because of the observed fluctuations in their densities. The three species showed higher densities within the canyon (especially *B. artica* and *R. glabra*). Also with relevant contributions to the dissimilarity between “location” groups were the mysid *Hemimysis abyssicola* (EP-Om-mic) and the amphipod *Synchelidum haplocheles* (SS-Pr-mei) with higher densities at BC (typically at <1200 m) and the euphausiid *Nematoscelis megalops (*EP-Pr-zoo) and the amphipod *Bathymedon longirostris* (SS-Pr-mei) with higher densities at OS. Other dominant species like the isopod *Belonectes parvus* (SR-Om-mic) at BC and the amphipod *Mediterexis mimonectes* (SR-Dt) at OS had lower contributions to the dissimilarity between “location” groups.

The higher contributions to the dissimilarity between “depth” groups were the epibenthic omnivore mysids *B. artica* and *H. abyssicola* with higher densities at sites <1200 m and the predators on zooplankton *R. caeca, R. glabra* (amphipods) and *N.megalops* (euphausiid) with higher densities at sites >1200 m. Lower contributions to the dissimilarity between “depth” groups were from the amphipod *Ileraustroe ilergetes,* also a predator on zooplankton, at the deeper sites and various species from different trophic groups typically associated to the sediment surface at the shallower sites (e.g. the cumacean *Leucon longirostris* - SR-Gr-mic*, the amphipod Bathymedon banyulsensis -* SS-Pr-mei and the amphipod *M. mimonectes* - SR-Dt).

Table 2.5.4 Breakdown of percent contributions from SIMPER analysis for comparisons between "location" (OS vs. BC) and "depth" (<1200 m vs.>1200 m). The taxa listed contribute more than 0.95% to the total similarity /dissimilarity (•: contributions lower than 0.95%). Numbers in bold mark the six dominant species in each category of location and depth.

	Density (ind.100m^{-2})				TG	% Contribution (Habitat)			% Contribution ("Water masses")		
	OS	**BC**	**<1200**	**>1200**		**OS**	**BC**	**OS vs. BC**	**<1200**	**>1200**	**<1200/>1200**
Total (averaged):	72.5	224.4	154.0	101.0		AS: 56.47	AS:44.48	AD:55.21	AS: 56.64	AS:52.99	AD:53.75
Amphipoda											
Rhachotropis caeca	**10.0**	**11.6**	**5.6**	**14.1**	EP-Pr-zoo	5.12	2.55	2.02	4.41	4.77	1.75
Rhachotropis glabra	**4.5**	**22.3**	**4.7**	**14.6**	EP-Pr-zoo	2.70	2.69	2.14	1.51	3.32	1.74
Rhachotropis rostrata	0.8	1.8	1.6	0.8	EP-Pr-zoo	1.30	1.19	●	1.43	1.20	●
Scopelocheirus hopei	0.0	2.5	1.9	0.1	SR-Om-mac	-	1.02	●	●	-	●
Bathymedon acutifrons	0.7	6.3	3.4	1.9	SS-Pr-mei	●	1.14	1.41	●	●	●
Bathymedon banyulsensis	1.0	3.1	**3.6**	0.4	SS-Pr-mei	1.33	●	●	2.23	●	●
Bathymedon longirostris	**4.8**	1.6	**3.6**	3.9	SS-Pr-mei	3.76	●	1.42	3.43	3.05	●
Oediceropsis brevicornis	0.6	0.7	1.3	0.1	SS-Pr-mei	●	●	●	1.60	-	●
Synchelidum haplocheles	0.1	**16.5**	**13.2**	0.1	SS-Pr-mei	-	0.97	1.67	●	-	1.14
Mediterexis mimonectes	**2.6**	0.9	2.9	1.5	SR-Dt	2.19	●	●	2.14	1.77	●
Bruzelia typica	0.8	1.2	1.2	0.8	EP-Pr-zoo	1.44	1.32	●	1.86	1.19	●
Ileraustroe ilergetes	2.6	4.5	0.9	**4.8**	EP-Pr-zoo	2.54	1.88	●	●	3.10	1.35
Cumacea											
Diastyloides serrata	0.9	5.1	3.3	1.6	SR-Gr-mic	1.41	1.71	1.16	1.24	1.59	●
Platyaspis typica	1.3	1.0	0.0	2.1	SR-Gr-mic	●	-	●	-	●	1.21
Leucon longirostris	1.9	1.3	3.2	0.6	SR-Gr-mic	1.62	1.45	●	3.11	●	1.37
Leucon macrohinus	0.5	2.1	1.2	0.9	SR-Gr-mic	●	0.94	●	●	-	●
Campylaspis spp	0.9	1.7	0.3	1.8	SS-Pr-mei	1.44	0.99	●	1.13	1.48	●
Isopoda											
Aspidarachna cf sekhari	0.6	0.1	0.8	0.2	SR-Om-mic	●	●	●	1.35	-	●
Belonectes parvus	2.0	**7.2**	0.5	**6.1**	SR-Om-mic	1.62	1.18	1.39		1.92	1.25
Gnathia sp	0.7	0.9	1.2	0.4	EP-Sp-fis	1.27	1.18	●	1.93	●	●
Mysida											
Boreomysis artica	**10.9**	**34.5**	**28.0**	**12.2**	EP-Om-mic	5.42	5.16	2.74	6.51	4.78	2.09
Hemimysis abyssicola	0.0	**68.2**	**54.5**	0.0	EP-Om-mic	-	2.12	3.49	1.15	-	1.86
Euphausiacea											
Nematoscelis megalops	**7.9**	4.3	1.4	**10.5**	EP-Pr-zoo	2.17	1.65	1.64	1.51	2.36	1.64
Contribution of the selected taxa:	77.8	88.9	89.8	84.5							

2.5.4 Discussion

Bathymetric patterns in deep-sea benthos have mostly been attributed to a decrease in food availability with depth (Rex et al., 2006). Three depth-related trends of benthic fauna have been described for deep-sea benthic communities: (1) an exponential decline in abundances with increasing depth (Rex et al., 2006); (2) a species diversity maximum at mid-slope depths (Rex and Etter, 2010); and (3) pronounced depth-related changes in benthic faunal composition (Carney, 2005). However, bathymetric patterns of abundance and diversity described for the deep-sea benthos (Rex and Etter, 2010) can be altered in submarine canyons and other geomorphic structures where they are subjected to a complex interplay of factors, such as increased nutrient input, heterogeneity in sediment types, topographic variability and current dynamics that determine the distribution and abundance of their benthic fauna (Levin and Dayton, 2009; McClain and Barry, 2010; Vetter et al., 2010; Cunha et al., 2011).

Our results confirmed the significance of the differences in composition and structure of the suprabenthic crustacean assemblages in relation to a putative canyon effect (“location” factor, canyon vs. slope) and to the influence of regional oceanographic processes (“depth” factor, <1200 m vs. >1200 m). Also important was the temporal variability, but the statistical analysis of this factor was hindered by the caveats associated with the sampling design (it was not possible to sample all depths and locations at the different occasions). The Blanes Canyon region has been extensively studied and there is a relevant accumulated knowledge on local hydrodynamic processes, primary productivity patterns and particle flux pathways as well as a detailed record on the occurrence of high-energy events over the last decades (Zuniga et al., 2009, Lopez-Fernandez et al., 2013a,b; Canals et al., 2013).

Previous studies in the Blanes Canyon have demonstrated that weather-driven high-energy events, such as river floods, storms and shelf water cascading have localized effects on current speed and particle fluxes and composition (Lopez-Fernandez et al., 2013a, 2013b) which, in turn, influence the spatial and temporal distribution patterns of the faunal assemblages (e.g. Romano et al., 2013; Almeida et al., in press). Canyon morphology (e.g. deeply incised into the continental shelf down to 1500 m depths; steep (>25º) and guilled walls in the western flank; Amblas et al., 2006; Zuniga et al., 2009; Jorda et al., 2013) alters the currents speed and direction and associated flux of particles and sediment properties (Lopez-Fernandez et al., 2013b; Zuniga et al., 2009) and the possible existence of depositional areas of organic matter at different locations in the canyon, as the result of the step-by-step transport of particles along the canyon, are important factors contributing to the differentiation of faunal assemblages inside the canyon (for instance by comparing sites BC900 and BC1500). High topographic heterogeneity was also related to spatial variability in other benthic compartments in the same canyon (Ramirez-Llodra et al., 2009; Ingels et al., 2013; Romano et al., 2013).

In our study, the biodiversity and distributional patterns of the crustacean suprabenthos were strongly affected by two important observations: i) the marked peaks of abundance at BC900 recorded in 2009 (mainly due to mysid aggregations) responsible for most of the bathymetric and canyon vs. slope differences; ii) the generalized enhancement in the abundance and biodiversity of the assemblages observed in 2012 that revealed important inter-annual variability.

Spatial variability

In 2009 the upper part of the canyon (900 m) presented the highest densities due to the numerical dominance of mysids while the remaining canyon sites presented much lower densities values. In 2009 the annual mean current speed at the canyon axis was higher at 900 m depth than 1500 m depth (7.0 and 4.2 $cm.s^{-1}$, respectively) with peaks above 20 $cm.s^{-1}$ registered several times during the year (Lopez-Fernandez et al., 2013b). In this year several storms were also reported for the area, however they affected only the upper part of the canyon (increased current speeds at depths <1200 m) (Sanchez-Vidal et al., 2012; Lopez-Fernandez et al., 2013b). In one hand, the increment of food in the canyon sediments from advective processes may explain the higher abundances of predators on meiofauna (several oedicerotids) observed at this depth. On the other hand, the productivity-disturbance regime (strong currents, high sedimentation rates and enhanced food sources) favored most the occurrence of highly mobile taxa such as the mysids (and to a lesser extent also eusirid amphipods) resulting in the markedly enhanced suprabenthic densities observed only at BC900. Similar situations were also observed at the canyon head subjected to high disturbance regimes (Almeida et al., in press).

At 900 m depth inside the canyon, the suprabenthic assemblages presented the lowest taxonomic and trophic biodiversity, especially, due to the dominance of omnivore mysids (e.g. *Hemymisis abyssicola* and *Boreomysis arctica*). These highly motile organisms may avoid disturbance events and they also respond to the variable hydrodynamic and particle flux regimes (e.g. lateral transport of organic matter inputs from the shelf regions, upper canyon reaches and gullies from the canyon flanks; Lopez-Fernandez et al., 2013b; Baldrighi et al., 2014) and changing trophic conditions by switching their feeding mode depending on flow energy). The well-known migratory behavior of mysids may lead to locally enhanced densities as was observed by Cartes and Sorbe (1995) in the Catalan Sea at intermediate depths. According to Trueman et al. (2014), such aggregations related to diel vertical migrations may be particularly relevant down to 1000 m depths while at greater depths these vertical migrations are much less evident.

In the adjacent slope at 900 m depth, the more stable conditions and high organic matter content (BC: approx. 2%; OS: 2-6%) could be associated to high quality of food sources (e.g. pelagic origin) (Lopez-Fernandez et al., 2013b) resulting in higher diversity. In accordance, the suprabenthic assemblages showed an important contribution of detritivores (e.g. the stegocephalid *Mediterexis mimonectes*) which were much less represented in the canyon sediments. At greater depths, suprabenthic diversity and density was similar between canyon and the adjacent slope. Some canyons and surrounding areas may show limited differences in sedimentary organic matter content and biochemical composition (Pusceddu et al., 2010a). Moreover, the influence of disturbance processes and flow energy is lower (Zuniga et al., 2009; Lopez-Fernandez et al., 2013b) and scarcity of food is more pronounced (Rowe et al., 1982), which could explain the increase of the relative abundance of predators on zooplankton, some with high motility, such as the eusirids *Rhachotropis* spp. and the synopiid *Pseudotiron bouvieri* (Cartes and Sorbe, 1999), a guild commonly observed in food limited environments (Tselepides et al., 2000). Given such conditions, in their lower sections, the faunal assemblages tend to be more similar to the ones in the surrounding environments (Cunha et al., 2011).

However, in occasions of high magnitude of disturbance events, other patterns may arise. This is evident by comparing sites at 1500 m which were sampled in all temporal occasions. While in 2009 densities and number of species were lower in the canyon and adjacent slope, in 2012 higher densities and number of species were observed in both habitats, with a peak registered inside the canyon. Potential reasons for these differences are discussed below.

“Canyon effect”

Suprabenthic assemblages in the Blanes Canyon region were clearly dominated by predators on zooplankton. The variety of food resources in the sediment and BBL, inside the canyon and adjacent slopes which are under the influence of the canyon, may cause the increase of different organisms exploiting the resources and thus, their predators. In fact, a large fraction of the samples collected with the epibenthic sledge was composed by copepods which may explain the high abundance of eusirids that feed on this group (Fanelli et al., 2009). Cartes et al. (1998b) also reported the dominance of copepods together with peracarids in suprabenthic assemblages.

Submarine canyons are areas of zooplankton, micronekton and fish aggregations that may be explained by the bio-physical coupling between currents and animal behaviour over abrupt topographies (Genin, 2004). In canyons the prevailing mechanisms leading to such aggregations include topographic blockage (after ascending from the deep canyon floor to the surface during the night, the organisms may be displaced by lateral advection and are subsequently topographically blocked during their morning descent), depth retention by swimming against prevailing currents (Genin, 2004) or funneling of the descending animals down the flanks into the canyon’s axis (Koslow and Ota, 1981). Macquart-Moulin and Patriti (1996) suggested the topographic blockage to explain the accumulation of migratory species in several canyons along the Mediterranean shelf. Abrupt topographies like the canyons can therefore have an important role in determining trophic interactions by generating “trophic focusing” i.e. subsidising high densities of prey that propagates up the food web (Genin, 2004). In the case of the studied assemblages in the Blanes Canyon the aggregations of zooplankton may favour the occurrence of suprabenthic predators on zooplankton and, in turn, the suprabenthos will also serve as a prey to higher trophic levels.

Inter-annual variability

In the NW Mediterranean Sea dense shelf water cascading (DSWC) has been recognized as a major particle transport mechanism off-shelf and downslope, along submarine canyons and neighbouring slopes, supplying the sedimentary slopes and basins (>2000 m) with fresh marine organic matter (Canals et al., 2006; Sanchez-Vidal et al., 2008; Pasqual et al., 2010). When DSWC takes place, the upper reaches of the canyons act as bypass zones during the event and the lower canyon, canyon mouth and adjacent slope receive large amounts of sediment and organic matter. The effect of intense events of DSWC on the flux and composition of particles can last for six months (Pasqual et al., 2010). Such events occur at a subdecadal scale (e.g. winter 1999; winter 2004/05; winter 05/06; Canals et al., 2006; Sanchez-Vidal et a., 2008). The arrival of such material may have different implications for deep-sea benthic ecosystems, by fuelling the deep seafloor with large amounts of bioavailable particles or by physically disrupting the benthic habitats (Pusceddu et al., 2010b). The Blanes Canyon is an important pathway in the down-slope flow of DSWC formed in the large shelf of the Gulf of Lion (Canals et al., 2013). The overall enriched fauna both in number of species and densities observed in October 2012 may be linked to a similar event that took place in the spring of 2012 in the Gulf of Lion (Durrieu De Madron et al., 2013; Mihanović et al., 2013; Sanchez-Vidal et al., 2015) and may have fuelled the deeper canyon and lower slope with large amounts of organic matter that persist for several months, including the Blanes Canyon region. Pusceddu et al. (2013) studied the effects of DSWC in deep-sea meiofaunal assemblages in the Cap de Creus Canyon and showed that the abundance and biodiversity declined after a similar event but recovered after six months after the cessation of the cascading. Company et al. (2008) observed that populations of the shrimp *Aristeus antennatus* declined immediately after the event but showed a strong recovery after 2-3 years of the cascading. It is likely that suprabenthos may also suffer an initial decrease followed by a relatively fast response taking in account their relatively shorter life cycles. The presence of high motile groups such as euphausiids in the slope (e.g. *Nemastocelis megalops*, zooplankton feeder) but also the increase in the relative abundance of omnivores (e.g. munnopsid *Belonectes parvus*) in the canyon only in 2012, may further support this link. In fact, several munnopsid species are specialized in benthic foraminifera which responds to the input of fresh organic matter deposition on the deep seafloor (Sorbe and Elizalde, 2014). Moreover, the observed turnover values (β-diversity) are likely reflecting the effect of DSWC on the canyon suprabenthic assemblages; the high turnover values determined mostly by species gain, may result from the quality of organic enrichment and the colonization of space after such a high-energy event.

2.5.5 Conclusions

The input of organic matter to the NW Mediterranean continental margins results from the complex interaction between topography and several oceanographic processes, with variable effects on the dynamic of suprabenthic assemblages. The quantity and composition of particles (lithogenic, biogenic) that reaches the deep NW Mediterranean seafloor is not consistent over time resulting in a highly variable suprabenthic fauna. Our results suggest that taxonomic and trophic diversity in the Mediterranean margins might be influenced by the abrupt topography and its interaction with hydrodynamic conditions (intensification of currents; variable intensity of disturbance/hydrodynamic events; food pulses linked to food availability). These are major drivers which influence the availability of food sources to the various faunal compartments (Ingels et al., 2013; Baldrighi et al., 2014), eventually propagating up the food web.

Suprabenthos is a heterogeneous benthic compartment with a variety of life cycles and functional traits. The activities of individual suprabenthic species allow a flexible community structure facing different environmental fluctuations that result in complex patterns in biodiversity. An analysis of biodiversity according to functional traits (motility) of the main groups resulted in more clear patterns. These observations are in accordance with several authors who found different trends according to the taxa considered and hypothesised that each group responds differently to the disturbance–productivity gradients in submarine canyons (Paterson et al., 2011).

Supplementary material

Table S.2.5.1. Relative abundance of the six most abundant species per depth strata in the Blanes Canyon and the adjacent slope.* pooled samples.

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Supplementary material

Table S2.5.1 Relative abundance of the six most abundant species per depth strata in the Blanes Canyon and the adjacent slope.* pooled samples.

OS900*		%	**BC900***		%
EP-Om-mic	*Boreomysis arctica*	18.8	EP-Om-mic	*Hemimysis abyssicola*	55.86
SR-Gr-mic	*Leucon longirostris*	11.4	EP-Om-mic	*Boreomysis arctica*	17.28
SR-Dt	*Mediterexis mimonectes*	8.97	SS-Pr-mei	*Synchelidium haplocheles*	12.06
EP-Pr-zoo	*Rhachotropis caeca*	8.83	SR-Gr-mic	*Diastyloides serratus*	2.86
SR-Om-mic	*Munnopsurus atlanticus*	4.54	SS-Pr-mei	*Bathymedon banyulsensis*	2.12
SS-Pr-mei	*Bathymedon longirostris*	4.09	SS-Pr-mei	*Bathymedon acutifrons*	1.97
		56.6			92.16
OS1050		%			
EP-Om-mic	*Boreomysis arctica*	20			
EP-Pr-zoo	*Rhachotropis caeca*	12.1			
SS-Pr-mei	*Bathymedon longirostris*	8.54			
EP-Pr-zoo	*Rhachotropis glabra*	5.66			
EP-Sp-fis	*Gnathia* sp	4.73			
SR-Om-mic	*Aspidarachna* cf *sekhari*	4.12			
		55.1			
OS1200*		%	**BC1200**		%
EP-Pr-zoo	*Rhachotropis caeca*	16.9	EP-Om-mic	*Boreomysis arctica*	26.19
EP-Om-mic	*Boreomysis arctica*	15.4	EP-Pr-zoo	*Rhachotropis glabra*	26.19
SS-Pr-mei	*Bathymedon longirostris*	13.5	EP-Om-mic	*Hemimysis abyssicola*	19.07
EP-Pr-zoo	*Rhachotropis glabra*	7.88	SR-Sc-mac	*Scopelocheirus hopei*	8.13
SS-Pr-mei	*Bathymedon banyulsensis*	4.03	EP-Pr-zoo	*Nematoscelis megalops*	7.5
SR-Gr-mic	*Leucon longirostris*	3.91	SS-Pr-mei	*Bathymedon acutifrons*	5.47
		61.6			92.55
OS1350		%			
EP-Pr-zoo	*Rhachotropis caeca*	16.6			
SS-Pr-mei	*Bathymedon longirostris*	11.6			
EP-Om-mic	*Boreomysis arctica*	10.8			
EP-Pr-zoo	*Rhachotropis glabra*	9.15			
EP-Pr-zoo	*Nematoscelis megalops*	6.44			
SS-Pr-mei	*Bathymedon banyulsensis*	5.82			
		60.5			
OS1500*		%	**BC1500***		%
EP-Pr-zoo	*Nematoscelis megalops*	18.5	EP-Pr-zoo	*Rhachotropis glabra*	31.78
EP-Pr-zoo	*Rhachotropis caeca*	16.5	SR-Om-mic	*Belonectes parvus*	9.52
EP-Pr-zoo	*Rhachotropis glabra*	12.4	EP-Pr-zoo	*Ileraustroe ilergetes*	7.44
EP-Om-mic	*Boreomysis arctica*	11.1	EP-Pr-zoo	*Rhachotropis caeca*	6.07
SS-Pr-mei	*Bathymedon longirostris*	4.96	EP-Om-mic	*Boreomysis arctica*	5.98
EP-Pr-zoo	*Ileraustroe ilergetes*	4.49	EP-Pr-zoo	*Nematoscelis megalops*	4.58
		68			65.37
OS1750		%			
EP-Pr-zoo	*Rhachotropis caeca*	13.8			
EP-Om-mic	*Boreomysis arctica*	12.3			
EP-Pr-zoo	*Ileraustroe ilergetes*	9.91			
SS-Pr-mei	*Bathymedon longirostris*	9.61			
EP-Pr-zoo	*Rhachotropis glabra*	7.21			
EP-Pr-zoo	*Nematoscelis megalops*	5.11			
		58			
OS2000*		%	**BC2000**		%
EP-Pr-zoo	*Nematoscelis megalops*	27.3	EP-Pr-zoo	*Rhachotropis caeca*	29.27
EP-Pr-zoo	*Rhachotropis caeca*	12.7	EP-Om-mic	*Boreomysis arctica*	12.05
EP-Om-mic	*Boreomysis arctica*	9.6	SR-Om-mic	*Belonectes parvus*	7.62
SR-Gr-mic	*Platysympus typicus*	7.92	EP-Pr-zoo	*Nematoscelis megalops*	5.92
EP-Pr-zoo	*Ileraustroe ilergetes*	5.68	EP-Pr-zoo	*Rhachotropis glabra*	5.21
SS-Pr-mei	*Bathymedon longirostris*	4.11	SR-Om-mic	*Ilyarachna cf longicornis*	4.22
		67.3			64.3

OS2250		**%**	**BC2250**		**%**
EP-Om-mic	*Boreomysis arctica*	26	EP-Om-mic	*Boreomysis arctica*	24.51
EP-Pr-zoo	*Rhachotropis caeca*	12.9	EP-Pr-zoo	*Rhachotropis caeca*	17.93
SS-Pr-mei	*Bathymedon longirostris*	6.98	SR-Gr-mic	*Vaunthompsonia caeca*	5.88
SR-Om-mic	*Belonectes parvus*	6.12	SR-Gr-mic	*Platysympus typicus*	4.94
EP-Om-mic	*Euphausia krohnii*	3.97	SS-Pr-mei	*Bathymedon longirostris*	3.94
EP-Pr-zoo	*Nematoscelis megalops*	3.14	SR-Pr-mei	*Procampylaspis armata*	3.62
		59.1			60.82

SECTION 3. GENERAL DISCUSSION

The vast area of the deep sea contrasts with the largely insufficient sampling of this biome. Although 60% of the surface of the earth is deep sea, less than 1% has been scientifically investigated (Clark et al., 2016). Bathymetric and large scale gradients in deep-sea biodiversity have been examined (Rex and Etter, 2010) and temporal patterns in deep-sea communities are comparatively less studied (Glover et al., 2010) but it is well-known that food-limitation is a major driver of such patterns (e.g. Smith et al., 2008). In this context, the Mediterranean Sea can be considered an optimal study area for investigating spatial patterns of deep-sea diversity and species distribution, due to the existence of a decreasing West-East productivity gradient and the relation of bathymetric trends with the nutrient input to the seafloor (Danovaro et al., 1999). Moreover, temporal variability of oceanographic and climate processes and the consequent effects in the deep-sea fauna are now being described and understood (Canals et al., 2013).

This Thesis is dedicated to the study of one of the most dynamic faunal compartments in the deep sea, the suprabenthos that, despite its importance for the ecosystem functioning is scarcely sampled. An overview of recent literature on suprabenthic composition and structure (or on certain suprabenthic taxa) of areas deeper than 200 m in European waters is shown in Table 3.1. Most of these studies were carried out at relatively shallow depths (<1000 m), and are rarely focused on the near-bottom vertical distribution of the fauna. In the western Mediterranean Sea, previous investigations targeted mainly island flanks and a few submarine canyons heads, including areas exploited for commercial fisheries. These works focused on the establishment of relationships between the occurrence of suprabenthos and megabenthos namely in terms of trophic resources (e.g. Cartes, 1998), suprabenthic production rates (e.g. Cartes et al., 2002a), isotopic analysis of suprabenthic species (e.g. Fanelli et al., 2009), zooplankton-suprabenthos dynamics (e.g. Cartes et al., 2008), distributional ecology in relation to environmental variables (e.g. Cartes et al., 2002b, 2003), and also biodiversity (Cartes et al., 2003; Cartes et al., 2011). Except for one study at 200-300 m in the eastern basin (Koulouri et al., 2013) quantitative studies on suprabenthic assemblages from other Mediterranean regions are lacking.

The results obtained in this Thesis present a basin-wide overview of the suprabenthos' biodiversity from the Mediterranean Sea. This study provides the first integrated dataset on the deep suprabenthic fauna spanning the three main Mediterranean regions and a large bathymetric range (from 1ºE to 26ºE; 600 m to 3000 m depth) of this oligotrophic system. The near-bottom vertical distribution, biodiversity, community composition, trophic structure were examined and interpreted in relation to their putative environmental drivers.

The investigations carried out in the framework of several research projects allowed to identify abiotic variables and anthropogenic pressures that affect species distribution and determine the spatial and temporal patterns of suprabenthic assemblages in submarine canyons and adjacent slopes of the northwestern Mediterranean Sea. On a regional scale, in the Catalan continental margin, this work further provided a comparison of the suprabenthic assemblages along the entire bathymetric range (400-2250 m depth) of the Blanes canyon and its adjacent slope, including the first data on these assemblages at lower-slope depths.

This Thesis identified several relevant issues for a better understanding of the deep-sea suprabenthic ecology:

- The different organisms and traits living in the seafloor-water column interface are subjected to the interplay of different environments. A consensus should exist on which fauna should be considered as suprabenthos to better compare and understand these assemblages.
- Studies focused on the interaction between suprabenthos and other benthic groups would be helpful to better understand biotic interactions especially in the Mediterranean Sea were the macrofauna–megafauna trophic relationships are relatively well known.
- The analysis of suprabenthos at the level of population dynamics would improve the knowledge of suprabenthic spatial and temporal patterns.
- Due to the importance of suprabenthic biological traits to the ecosystem processes in the deep sea, this group should be considered in model studies to understand ecosystem functioning and predictions of changes mediated by human effects.

Below are some remarks on the caveats associated to the sampling constraints in the study of deep-sea suprabenthos followed by an overview of the main findings in the context of the current knowledge on the biodiversity of this important faunal compartment in the Mediterranean and Atlantic deep waters. Some final remarks conclude this Thesis.

Sampling constraints

Sampling the suprabenthic fauna is limited by technical difficulties in collecting samples efficiently in the water layer just above the seafloor (Mees and Jones, 1997; Koulouri, 2014). According to Mees and Jones (1997) “satisfactory” samples can be taken with plankton nets mounted on sledges. A difficulty when towing these nets at relatively low speed at the seafloor is that the ability to capture the animals may vary largely among taxa depending on their mobility. As an example, Lasenby and Sherman (1991) observed that good swimmers such as mysids avoid capture by swimming in front of the sledges. Consequently, density values of such animals may often be underestimated. Several authors (Huberdeau and Brunel, 1982; Fossa, 1985, 1986), using different suprabenthic sledges concluded that a general flaw of this type of gear is that the lowermost centimeters above the sediment, which may be very rich, are not sampled. On the other hand, the turbulence caused by the contact of the sledge with the seafloor may resuspend the uppermost layer of sediments and their associated fauna leading to the collection of animals that live both on top (wanted) and inside the sediment (unwanted). Therefore, to include a given taxon as suprabenthos implies a certain margin of error depending on whether or not there is available information on its biology and autoecology. Even so, most of the animals usually captured by an epibenthic sledge and considered as suprabenthos are known as not having a strictly benthic life style.

Studying the suprabenthos in deep-water environments imposes additional problems. The ecological traits of the species, their typical low densities, small body sizes, the high species richness and occurrence of many rare species in deep-sea assemblages requires more and larger sampling to describe the fauna than in shallow waters (Jamieson et al., 2013). Sampling the deep sea is extremely difficult, time consuming and expensive because of the great distance from the surface to the seafloor and the high hydrostatic pressure. Towing or lowering equipment on thousands of meters of wire can take several hours and requires specialized equipment and experienced operators. Also, the adverse weather conditions often experienced at sea or technical problems may result in the loss of time, sampling failure or damaged specimens during recovery. Given this, an optimal sampling design with sufficient replication required to characterize an area of the seafloor, assess variability as well as to increase the statistical validity of the data and the power of hypothesis testing is rarely achieved when working in the deep-sea. Accordingly, the lack of spatial and temporal replication represents a fundamental caveat in the analysis of my data both at basin and regional scales. Nevertheless, several authors tested the replicability of suprabenthic sledge samples (Hesthagen and Gjermunsen, 1978; Schnack, 1978; Brattegard and Fossa, 1991) and concluded that, in a cost-efficient context, these samples are representative as long as towing distance is adequate.

Migratory behavior

Suprabenthos species may perform tidally-phased (e.g. estuarine environments) or diel (e.g. marine environments) migrations and therefore it is recommended that suprabenthic sampling should be carried out during daytime when the organisms are concentrated near the seafloor (Sorbe and Elizalde, 2014). Again, when sampling in the deep-sea, the timing of the offboard operations is set by a series of logistic constraints and, as happened with my samples, the time of sampling is often not consistent between cruises or even within the same cruise. Nevertheless, there is accumulating evidence that the suprabenthos migratory behavior may be attenuated or even supressed with increasing depth. In this context, eventual nocturnal migrations may be considered a relatively minor factor influencing bathyal suprabenthos distribution and thus affecting suprabenthic sampling at greater depths.

Several authors studying diel activity patterns for deep-water suprabenthos demonstrated a limited amplitude of nocturnal vertical migrations of most suprabenthic organisms (Koulouri et al., 2013) or their confinement to the vicinity of the seafloor (Kaartvedt 1986; Frutos and Sorbe, 2014). With increasing depth, even the highly motile mysids remain mostly restricted to the near-bottom with very few individuals captured some meters (ca. 5 m) above the seafloor (Cartes and Sorbe, 1995, Cartes, 1998).

Recently Trueman et al. (2014, study on temperate waters) proposed the 1000 m depth as the maximum daytime depth of the DVM (diel vertical migrators) community, where some suprabenthic species are included (e.g. mysids, amphipods; Maycas et al., 1999). At depths shallower than 1000 m the DVM community is key for the active transport of carbon and other nutrients from the surface to the seafloor whereas at greater depths bentho-pelagic-feeding fishes are instrumental in capturing carbon from the DVM community and its subsequent transfer to the demersal and benthic community. In subtropical waters, van Haren and Compton (2013) report DVM down to 1600 m although with marked decreasing daytime periods at the bottom for these greater depths.

Trophic structure

Trophic relations in the deep sea have only in recent years started to be evaluated in detail. Due to the wide diversity of functional groups found within suprabenthic taxa, the causes of ecological responses can be more easily interpretable working at trophic/functional level, especially in the Mediterranean Sea, where food limitation is the most important driver in the deep-sea benthic communities (Danovaro et al., 2010). Of course, there are limitations to this type of analyses because of the lack of studies on the feeding habits and auto-ecology of deep-sea peracarids (Cartes and Sorbe, 1999). Nevertheless, the ongoing study of the trophic relationships of suprabenthos and megabenthos in the Mediterranean Sea, mostly in its upper slopes, contributed to the knowledge of the trophic habits of dominant suprabenthic species in the Mediterranean Sea (e.g. Cartes et al., 2001; Fanelli et al., 2009) which was fundamental to support the detailed analysis of the trophic structure and diversity at species level.

When the trophic structure of the assemblages was analysed patterns emerged that provided complementary information to the one obtained from the taxonomic structure. The interpretation of both taxonomic and trophic data lead to a better understanding on the changes in structure and biodiversity of the crustacean suprabenthic assemblages in the different areas investigated as well as on the community response to the varying environmental conditions. Trophic structure analyses revealed to be a good tool and should be more commonly used to assess the drivers of these assemblages.

Biological interactions with other faunal components

Not only environmental drivers influence the distribution, structure and diversity of deep-sea suprabenthic assemblages but also the interaction with other fauna. For example, in the South Shetland Islands and Bransfield Strait (Antartica), the absence of epibenthic three-dimensionally communities were indicated as an important driver in suprabenthic community structure, resulting in high dominance of a few species (San Vicente et al., 2007). In the western Mediterranean, suprabenthic species are relevant items in the diet of megabenhtic predators (e.g. Carrassón and Cartes, 2002; Sardà and Cartes, 1997). Higher abundances of predators were associated to high suprabenthos abundances (D’Onghia et al., 2004). Moreover, Cartes et al. (2010) suggested a relation between the migratory movements of mysids and the aggregations of one of their predators, the rose shrimp *A. antennatus*. In the fishing grounds studied in this thesis, physical disturbance was identified as an important factor determining the structure of the suprabenthic assemblages, but the removal of predators by the fishing gear was also suggested as a factor to be accounted for. Biotic interactions are pointed as a major modifier of community patterns (Levin et al., 2001) but the underlying mechanisms of such interactions in the deep sea remain poorly understood.

Large-scale patterns

A high range in suprabenthic densities was found in this study in agreement with previous studies in the western Mediterranean and northeast Atlantic region (see Table 3.1 for values and references) and this was attributed to different environmental conditions of the investigated slope systems (e.g. food availability, hydrodynamic regime) and also to species-specific behavior. However, comparisons with suprabenthic assemblages from other regions are limited by the differences in sampling methodologies and whether or not the same taxonomic groups are included in the suprabenthos. Nevertheless, densities and number of species were in general lower than the ones found in the northeast Atlantic region using similar sampling gears at comparable depths. This is a generalized trend in the Mediterranean deep-sea fauna due to its evolutionary history as well as its physiography, hydrological properties and oligotrophy (Bouchet and Taviani, 1992). In fact, oligotrophy was identified as an important determinant of decrease in densities along the longitudinal gradient of the bathyal Mediterranean Sea.

However, the results on biodiversity have proved to be more complex. Danovaro et al. (2010) had already reported that several deep-sea benthic components displayed variable diversity values at different longitudes, without any significant pattern across the regions investigated. Given the different factors (i.e. biogeography, habitat characteristics, environmental variability, disturbance, metapopulation dynamics) and the insufficient knowledge on the mechanisms that may affect biodiversity, the interpretation of the results requires some degree of speculation.

Most studies on the structure and biodiversity of suprabenthos have been focused on the total assemblage collected by the sledge or only in the water layer close to the seafloor as the upper layers are generally characterized by low individuals. Usually when the stratified distribution above the seafloor is analyzed, it focuses mainly on the analysis of densities (Dauvin et al., 1995, Sorbe, 1999) and rarely on the suprabenthic near-bottom vertical structure and biodiversity (Cunha et al., 1997). In this Thesis, the study of the small-scale vertical distribution of the Mediterranean suprabenthos along a large longitudinal and bathymetric scale showed structural fluctuations of the different suprabenthic components and functional traits (dispersion capacities, motility, food consumption, bottom dependence) to changing environmental conditions, that could only be revealed by the analyses of the fauna in relation to its vertical distribution in close vicinity to the seafloor. Moreover, the analysis of β-diversity along both bathymetric and longitudinal gradients revealed other patterns not detectable by estimating the α-diversity alone. In the future, a sampling design including both suprabenthos and zooplankton (for instance, by analysing zooplankton and suprabenthos abundance and biodiversity) may shed light on the trophic interactions and mechanisms behind these complex patterns.

Regional temporal and spatial patterns

The increased multidisciplinary research projects for the study of the northwestern Mediterranean Sea canyons in the last two decades, allowed an integrative approach into the knowledge of biodiversity, structure, function, dynamics and anthropogenic impacts on these systems. The research effort in the Blanes Canyon region during the past decades revealed that this canyon experiences strong spatial and temporal variability in current speeds and particle transport along the canyon axis, linked to major energy-driven events like storms, river discharges, as well as dense water formation during winter, while the adjacent open slope is less affected by these hydrodynamic regime fluctuations (Zuniga et al., 2009; Sanchez-Vidal et al., 2012; Canals et al., 2013; Lopez-Fernandez et al., 2013).

The occurrence of DSWC, a sub-decadal climatic process in the region, was suggested as a relevant factor leading to inter-annual variability. This high-energy phenomenon responsible for the transport of fresh organic matter to the lower slopes and basins is thought to enhance the productivity of various faunal compartments (Company et al., 2008; Canals et al., 2013) and was likely related to the generalized increment in the suprabenthic densities and number of species observed in 2012. My data was not adequate to infer on smaller-scale temporal variability but previous studies in the Bay of Biscay (Frutos and Sorbe, 2014; Sorbe and Elizalde, 2014) showed a clear seasonal response of the suprabenthos related to fluctuations in surface primary production. In the future, there is the need to obtain larger and more complete biological time-series in order to elucidate temporal variability in deep-sea assemblages.

In general, studies on canyon and nearby environments are focused on bathymetric gradients and comparisons to the adjacent slopes which are often limited to a narrow depth range, mostly restricted to the upper reaches and intermediate depths (e.g. Vetter et al., 2010 and references therein). In the relatively well-studied Bay of Biscay suprabenthos' studies covering a depth range of 175-1000 m showed decreased abundances and increased biodiversity at bathyal depths (Frutos and Sorbe, 2014; Sorbe and Elizalde, 2014) in agreement with the general patterns for benthic assemblages (Rex and Etter, 2010). As mentioned before, the sampling constraints in deep-sea habitats and in particular the difficult access to submarine canyons, result frequently in the lack data to perform a comprehensive integrative approach. This work provides novel data on the structure and biodiversity of suprabenthic assemblages spanning the entire bathymetric range of a submarine Mediterranean canyon, further establishing relationships between the physical environment and community structure and biodiversity. The assemblages showed high variability, especially at shallowest sites subjected to higher intensity and frequency of energy-driven events. The high abundances and dominance of motile taxa in localized areas of increased disturbance at the head and upper reaches of the canyon accentuated the differences from the slope assemblages both in terms of taxonomic and trophic diversity (for instance the relatively clear trend of decreasing trophic diversity with increasing depth observed in the slope was obscured in the canyon by the extremely low values at 900 m). With increasing depth, intensity and frequency of the disturbance events was lower and its putative effects were less evident or even absent lessening the differences in diversity of the assemblages from the canyons and adjacent slopes (Fig. 3.1).

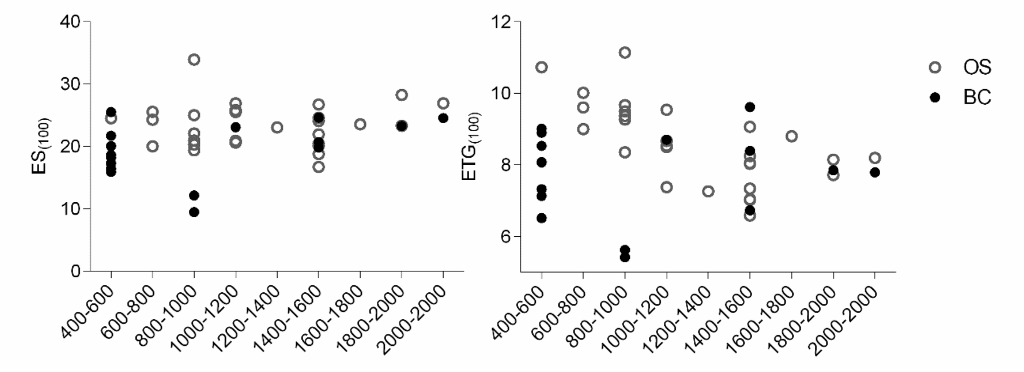

Figure 3.1 Expected number of species and trophic guilds of peracarid suprabenthic assemblages in all sites from the RECS, PROMETEO and DM cruises the Blanes Canyon and adjacent open slope.

It is noteworthy that the “canyon effect”, often referred in the literature, was only particularly evident for the studied assemblages at depths shallower than ca. 1000 m where the highest densities of suprabenthos were detected. The mechanisms leading to such aggregations cannot be completely elucidated by the available data. However, these findings are compatible with previous observations suggesting the importance of enhanced local production and/or of the bio-physical coupling processes between oceanographic factors and swimming behavior of the fauna, further modulated by topography (reviewed by Genin, 2004).

The northwest Mediterranean margin is characterized by several canyons incising a relatively narrow shelf and steep slope. This abrupt topography favoring accumulations of prey organisms (“trophic focusing”, Genin, 2004), particularly in a marine system characterized by its oligotrophy, has an important role in propagating high biomasses up the food web and often sustaining productive fisheries.

In the Blanes Canyon region, suprabenthos is part of the diet of the deep-sea rose shrimp *Aristeus antennatus* (Risso, 1816), which has been regularly targeted by crustacean trawlers for the past seven decades at depths from 300 to 900 m (Sardà and Cartes,1997; Sardà et al., 2009; Gorelli et al., 2014). The few studies focused on fishing impacts on suprabenthic assemblages were only performed in coastal areas (Koulouri et al., 2005; Cartes et al., et al., 2007). In this Thesis I showed that although species may respond differentially according to their functional traits, the deep-sea suprabenthic assemblages were overall highly resilient to trawling disturbance, even more in areas exposed to natural disturbance. My results also suggest that trawling may induce predation relief by removing large biomasses of predators.

Final remarks

A main concern of the deep-sea research is the effect of human action in the marine ecosystems. The Mediterranean Sea trawling fisheries currently extend to almost 1000 m water depths and the effects of this activity in the deep-sea already became evident by the degradation of sedimentary habitats and faunal paucity (Clark, 2015). There is also increasing evidence that the Mediterranean deep-sea fauna is affected by climatic phenomena modifying the organic carbon fluxes to the seafloor and the physico-chemical characteristics of the deep waters (e.g. Danovaro et al., 2001; Cartes et al., 2015). As it is recurrently observed in many deep-sea studies, the results of my Thesis suggest that suprabenthic assemblages are highly influenced by climate and near surface ocean processes. They are also affected by high levels of trawling pressure and complex interactions with natural disturbance. The ongoing process of global climate change, the growing human populations and natural resources demand are expected to exert an increasing pressure on deep-sea assemblages. It is therefore imperative to consider the synergistic effects of these multiple stressors in future research on the deep Mediterranean Sea preferably through integrated multidisciplinary investigations and ecosystem-based approaches.

Table 3.1 Overview of recent literature on suprabenthic community structure and biodiversity >200 m depth. All studies applied epi- or suprabenthic sledges for sampling. RP: Rothlisberg and Pearcy sledge (Rothlisberg and Pearcy, 1977); SS: Sorbe sledge (Sorbe, 1983); MG: Macer-GIROQ sledge (Dauvin and Lorgere, 1989); SH: Sanders and Hessler sledge (see Marquiegui and Sorbe, 1999); N: net attached to a bottom trawl. Note: mesh size is in millimeters. * not considered the all assemblage (Peracarida or Suprabenthos); **: no acess to the publication; ***: biomass data; -: no data.

Source	Sledge	Mesh size (mm)	Depthrange (m)	Fauna	Nº of hauls	Density (ind-100m^{-2})	Nº of species	Diversity (H')
NE Atlantic								
Norwegian Sea and fjords								
Buhl-Jensen (1986)	RP	0.5	147-550	Amphipoda*	-	-	-	-
Fosså and Brattegard (1990)	RP	0.5	32-1260	Mysida*	-	-	-	-
Porcupine Seabight and Meriadzek Terrace (N Bay of Biscay)								
Vanquickelberghe (2005)	SS	1	200-1250	Peracarida	16	~100-14000	17-102	1.93-3.84
Meriadzek Terrace (N Bay of Biscay)								
Dewicke (2002)	SS	2	200-700	Suprabenthos	6	226-1300	67-108 (214)	-
Cap-Ferret area (SE Bay of Biscay)								
Elizalde et al. (1991)	MG	0.5	346-1099	Mysida*	-	-	-	-
Elizalde et al. (1993)	MG	0.5	425-1043	Suprabenthos	3	271.8-1383.1	63-116 (187)	2.78-5.53
Dauvin et al. (1995)	MG	0.5	346-3070	Suprabenthos	15	189-1588	-	-
Dauvin and Sorbe (1995)	MG	0.5	346-1099	Amphipoda*	-	-	-	-
Sorbe and Weber (1995)	SS	0.5	392-717	Suprabenthos**	-	-	-	-
Sorbe (1999)	MG	0.5	2400,3000	Suprabenthos	8	283.3-525.3	-	-
Sorbe and Elizalde (2014)	SS	0.5	386–420	Suprabenthos	11	82-3199	31-76 (109)	2.30-4.01
Capbreton area (SE Bay of Biscay)								
Marquiegui and Sorbe (1999)	SH	0.5	1000	Suprabenthos	2	-	63	3.04-5.03
Corbari and Sorbe (2001)	SH	0.5	162-987	Suprabenthos**	-	-	-	-
Sorbe et al. (2010)	S	0.5	391-405	Suprabenthos	1	391	56	-
Frutos and Sorbe (2014)	SS	0.5	175-1000	Suprabenthos	8	752-2640	48-102 (205)	3.83-5.72

Source	**Sledge**	**Mesh size (mm)**	**Depthrange (m)**	**Fauna**	**Nº of hauls**	**Density (ind-100m^{-2})**	**Nº of species**	**Diversity (H')**
Asturian Central Coast (S Bay of Biscay)								
Anadón (1993)	SH	2	50-1347	Mysida*	-	-	-	-
Portuguese continental margin (off Aveiro)								
Cunha et al. (1997)	SS	0.5	299	Suprabenthos	1	916.1	74	4.15
Mediterranean Sea								
Catalan Sea (NW Mediterranean)								
Cartes et al. (1994)	MG	0.5	389-1859	Eucarida*	-	-	-	-
Cartes and Sorbe (1995)	MG	0.5	389-1859	Mysida*	-	-	-	-
Cartes and Sorbe (1996)	MG	0.5	389-1808	Cumacea*	-	-	-	-
Cartes and Sorbe (1997)	MG	0.5	389-1859	Cumacea*	-	-	-	-
Cartes (1998)	MG	0.5	389-1355	Suprabenthos	21	24.4-2150.1	-	-
Cartes and Sorbe (1999)	MG	0.5	389-1859	Amphipoda*	-	-	-	-
Cartes et al. (2002b)	MG	0.5	189-1645	Suprabenthos	9	24.7-190.2	-	-
Cartes et al. (2009)	MG	0.5	524-670	Suprabenthos	-	530.6-538.8	-	-
SW Balearic Islands (SW Mediterranean)								
Cartes et al. (2001)***	MG	0.5	210-1752	Suprabenthos	-	-	-	-
Cartes et al. (2008, 2011)	MG	0.5	150-750	Suprabenthos	46	10.0-277.7	8-57.8 (187)	1.55-3.23
Balearic Islands and Catalan Sea								
Cartes et al. (2003)	MG and N	0.5	249-1622	Peracarida	27	-	34-144	1.27-5.16
Eastern Mediterranean								
Koulouri et al. (2013)	TS	0.5	300	Suprabenthos	3	12-248	8-42	-

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