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ASSESSMENT OF INDIRECT IMPACT OF BOTTOM TRAWLING ON COLD-WATER CORALS IN BLANES CANYON

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Summary

Bottom trawling is the most common form of extensive anthropogenic physical disturbance in the marine environment. Due to technical advancements and search for new fishing grounds, the depth limits for this fishing practice have extended below 1 000 m. In the northwest (NW) Mediterranean Sea, bottom trawling usually takes place on the continental shelf and slope, as well as on submarine canyon flanks and rims, where one of the target species is the blue and red deep sea shrimp *Aristeus antennatus*. Ploughing of fishing gears over the seabed resuspends large amounts of soft sediments, which are then further transported through submarine canyons towards deep sea environments in the form of turbidity currents or high suspended sediment concentration (SSC) nepheloid layers. Such sediment transport processes expand beyond fishing grounds, thus exerting a negative impact on organisms that were initially not influenced by the direct impacts of bottom trawling. This is especially important for benthic filter feeding organisms as the increased SSC can cause clogging of their feeding apparatus or hypoxia when sediment covers their bodies. Submarine canyons serve as a significant habitat for cold-water corals (CWCs), which are bottom-dwelling organisms that feed on suspended particles and can flourish on the walls of the canyon. The complex morphology of submarine canyons, as well as the diverse composition of their substrates, and their interaction with the hydrodynamics create favourable circumstances for the growth and distribution of CWCs. These are slow-growing, long-living, and structurally complex organisms particularly vulnerable to anthropogenic impacts. Alongside, they form dense aggregations of one or several species, where other organisms such as fish, crustaceans, gastropods, molluscs find shelter, feeding, and/or mating grounds. Several CWC species are considered endangered species in the Mediterranean Sea and are included in the IUCN Red list, the Barcelona Convention and in the LESRPE (Listado de Especies Silvestre sein Régimen

de Protección); this further amplifies the importance of filling knowledge gaps for these species in a manner that can help future conservation and spatial management efforts. This thesis contributes to these efforts using Blanes Canyon (NW Mediterranean) as a case study, since important fishing grounds are found on its canyon flanks and rims, while the diversity, extent and vulnerability of megabenthic species in the canyon was up this to date unknown. In order to do this, research cruises (ABRIC 1 and ABRIC 2) were conducted in Blanes Canyon, where CTD casts and water sampling were performed along the canyon, as well as ROV video transects and faunal sampling by means of ROV.

The second chapter is dedicated to the description of the megabenthic communities found on the canyon walls along the canyon, with a focus on CWCs belonging to the orders Scleractinia, Antipatharia, Scleralcyonacea, and Malacalcyonacea. Based on the extensive high-resolution dataset acquired, a canyon gradient has emerged, where more solid corals (Scleractinia) were found in the more dynamic canyon head, whereas moving away from the canyon head, especially in the east canyon tributary, orders Antipatharia, Scleralcyonacea, and Malacalcyonacea prevail. This can be attributed to the changing environmental factors along the canyon, in terms of current speed, food availability, and sediment dynamics. Moreover, this study confirms Blanes Canyon as an important habitat for 13 species of CWCs, along with several rare species of sponges, molluscs, ascidian and fish.

The third chapter is dedicated to the water masses found in Blanes Canyon and the characterization of bottom trawling-induced nepheloid layers. Water samples taken in two distinct years across the canyon areas with and without bottom trawling activity show significant differences, indicating that bottom trawling, alongside other sediment dynamic processes, influence the quality of suspended matter arriving to the canyon interior.

The fourth chapter is dedicated to experimentally evaluating the effects of increased SSC on CWC survival, growth, and physiology (respiration and excretion). Six relevant CWCs were chosen and subjected to three distinct, laboratory-based SSC over 9 months. The results of this study show that the responses are species-specific, where survival was the best indicator as physiology did not change significantly. Colonial scleractinians and antipatharians were most affected by the SSC, while octocorals and cup corals were not disturbed by increased SSC.

Overall, this thesis has filled in knowledge gaps on CWC distribution, environmental preferences, and corroborated the importance of submarine canyons as habitat for CWCs, highlighting Blanes Canyon as a significant reference habitat for future studies. Moreover, this study emphasizes the vulnerability of megabenthic species and the indirect negative effect, i.e., high SSC, of bottom trawling, that extends beyond the immediate fishing grounds. This finding can eventually inform policy decisions when considering conservation and mitigation measures.

"In the Ramtop village where they danced the real Morris dance, for example, they believed that no one is finally dead until the ripples they cause in the world die away.

Until the clock he wound up winds down, until the wine she made has finished its ferment, until the crop they planted is harvested.

The span of someone's life, they say, is only the core of their actual existence."

Reaper Man from Terry Pratchett

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1. CHAPTER 1: General introduction

1.1. Cold-water corals (CWC)

Cold-water corals (CWC) is an umbrella term for species belonging to the class Anthozoa, more specifically to the orders Antipatharia, Scleractinia and subclass Octocorallia, alongside family Stylasteridae from class Hydrozoa (Roberts, 2009; Altuna and Poliseno, 2019; McFadden et al., 2021). As the name suggests, CWCs are typically found in cold waters (4 - 12°C), however there are exceptions, e.g. in the Mediterranean Sea, where CWCs can be found at higher temperature (~ 14°C) (Roberts, 2009; Hayes et al., 2019). These organisms are usually found bellow 200 m depth, or shallower in higher latitudes, thus inhabiting a wide depth range between 50 - 4000 m depth (Roberts, 2009; Aymà et al., 2019). They can be encountered in a palette of different habitats and seascapes, including the continental shelf and slope, submarine canyons, seamounts and escarpments (Davies and Guinotte, 2011; Chimienti et al., 2019; Puig and Gili, 2019). Most CWCs need hard substrate to settle and grow, while some Octocorallia such as bamboo corals and sea pen are found on soft sediment (Pierdomenico et al., 2018; Altuna and Poliseno, 2019).

When other environmental conditions are met, such as food availability and relatively strong currents, CWCs can proliferate, forming dense populations. These can have the form of coral mounds, in the case of colonial scleractinians which build hard skeletons, or they can also be dense mono- or multi-species aggregations of more erect species like octocorals and antipatharians, also known as coral gardens (Bullimore et al., 2013; Buhl-Mortensen et al., 2016). In those cases, CWCs increase habitat heterogeneity of the surrounding environment, increasing the breadth and diversity of ecological niches (Buhl-Mortensen et al., 2010). Moreover, CWC mounds and dense coral gardens can change the environmental conditions, altering bottom current flow, trapping particulate matter and sediment (Jones et al., 1994; Soetaert et al., 2016; Rossi et al., 2017; Orejas et al., 2022) and fuelling the local carbon cycle (Oevelen et al., 2009; Rix et al., 2016). Collectively, these functions attract other species which use this space in different ways, such as feeding, mating grounds or shelter (Costello et al., 2005; Demopoulos et al., 2014; Henry and Roberts, 2017). CWCs are also known to attract commercial species, such as fish and crustaceans, at different stages of their life, functioning as feeding, mating grounds and nurseries (Baillon et al., 2012; D'Onghia, 2019; Rueda et al., 2019).

As suspension feeders, CWCs feed on a variety of food sources (Sherwood et al., 2008; Maier et al., 2023). These sources can become available through different mechanisms including sinking and fast transfer from the surface through downwelling (Davies et al., 2009), as well as through resuspension caused by near – bottom transport (Riisgård and Larsen, 2017), and zooplankton vertical migration (Guihen et al., 2018). Zooplankton has been identified as key player in their metabolism (Carlier et al., 2009; Naumann et al., 2011; Maier et al., 2019b; Rakka et al., 2021).

In order to maximize prey capture in given environmental conditions, CWCs have developed a variety of growth forms, from long whip colonies to elaborate, bushy colonies and extensive coral mounds (Lartaud et al., 2019; Sanna and Freiwald, 2021). Alongside morphological diversity, they also display various forms of skeletal support from solid aragonite forms, sclerites based on Mg-calcite or carbonate hydroxyapatite, as well as scleroproteins and chitin (Goldberg, 1973; Bayer and Macintyre, 2001; Tambutté et al., 2011).

Alongside, different growth rate strategies are employed, but it is generally considered that CWCs are slow-growing, long living animals (Andrews et al., 2002; Adkins et al., 2004; Carreiro-Silva et al., 2013; Bennecke et al., 2016) Similarly, many CWCs are known to have low reproductive output and recruitment success, which adds an additional layer of vulnerability (Lacharité and Metaxas, 2013; Waller et al., 2023). Overall, living in colder, food-limited environment than their shallow water counterparts makes CWCs more vulnerable to anthropogenic impacts, such as removal or injury and habitat loss from fishing activities and fossil fuel extraction, as well as expected impacts from deep sea mining (Ragnarsson et al., 2017). As a result, CWCs are recognized as Vulnerable Marine Ecosystems (VME) (FAO, 2009) and protected under several international agreements, including IUCN Red List (Otero et al., 2017), Barcelona Convention (UNEP/MAP-SPA/RAC, 2018) and specifically important for Spain, LESRPE (Listado de Especies Silvestre sein Régimen de Protección) (Ministerio de Medio Ambiente, y Medio Rural y Marino, 2011).

1.2. CWC in the Mediterranean Sea

The Mediterranean Sea is a semi-enclosed sea, characterised by high seawater density ($\sigma_t > 28.5$ kg m^{-3}), high salinity ($S \geq 38$) and relatively high temperatures ($T > 13$ºC) (Millot, 1999; Tanhua et al., 2013). Due to this, for many years it was considered not ideal for CWCs, as the seawater density was outside of what was considered optimal (Dullo et al., 2008). However, an increase in studies employing advanced technologies such as Remotely Operated Vehicles (ROV) during the last 20 years have confirmed the Mediterranean Sea as an important environment for CWCs (Tursi et al., 2004; Freiwald et al., 2009; Angeletti et al., 2019; Evans et al., 2019). Based on fossil records, we know that over the last 20 Ma there have been several periods of colonial scleractinian proliferation and decline in the Mediterranean Sea, including changes in dominant species (Rebesco and Taviani, 2019; Vertino et al., 2019). At the same time, the fossil records are mostly available for scleractinian species, while octocorals and antipatharians are infrequent in fossil records (Quattrini et al., 2020). This can cause bias towards one type of CWCs, while recent studies, not only in the Mediterranean but also globally, have acknowledged the relevance of octocoral and antipatharian species in building diverse assemblages (Gori et al., 2017; Bo and Bavestrello, 2019). Moreover, higher resilience to a variety of environmental conditions has been shown to be a driver of octocoral distribution when the conditions are not ideal for scleractinian corals (Ruzicka et al., 2013; Quattrini et al., 2020).

For the purpose of this thesis, we will focus on CWCs associated with hard substrate, without considering sea pen fields and bamboo coral gardens that are typically found on soft bottoms (Pierdomenico et al., 2018). In the Mediterranean Sea, CWCs are mostly found below 200 m depth, inhabiting different geomorphic features such as continental slope, submarine canyons and seamounts (Chimienti et al., 2019 and references within). The Levantine Intermediate Water (LIW) has been identified as an important pathway of CWC distribution for several reasons (Chimienti et al., 2019; Hayes et al., 2019). This water mass is the only intermediate water mass that connects the East and West Mediterranean, potentially being the means of genetic exchange between the two basins, as well as within each basin (Boavida et al., 2019a; Johnston and Larsson, 2019). As it flows at intermediate depth, it washes over hard substrates that are suitable for CWC growth, such as the above-mentioned geomorphic features. The hydrodynamic regime is enhanced at those features, leading to currents which can prevent sediment deposition and supply food.

Regarding corals that build hard skeleton, i.e. belonging to the order Scleractinia, the main species found in the Mediterranean are *Desmophyllum pertusum* (Linnaeus, 1758) (previously known as *Lophelia pertusa* (Addamo et al., 2016)) (Fig. 1.1A), *Desmophyllum dianthus* (Esper, 1794) (Fig. 1.1C), *Madrepora oculata* Linnaeus, 1758

(Fig. 1.1B)and *Dendrophyllia cornigera* (Lamarck, 1816). Based on our current knowledge, the main reef-building colonial scleractinian in the Mediterranean is *M. oculata*, while e.g., in the north Atlantic Ocean, *D. pertusum* is the main mound building species. More studies are needed to fully understand the connectivity of different populations of these species (Arnaud-Haond et al., 2017; Boavida et al., 2019a, 2019b)

Compared to Scleractinia species, in the Mediterranean deep sea more species are found belonging to Octocorallia and Antipatharia (Grinyó et al., 2016; Gori et al., 2017; Bo and Bavestrello, 2019; Grinyó et al., 2020). Several common species found along the Mediterranean belonging to Octocorallia subclass are: *Callogorgia verticillata* (Pallas, 1766) (Fig. 1.1D), *Acanthogorgia hirsuta* Gray, 1857 (Fig. 1.1E), *Viminella flagellum* (Johnson, 1863), *Muriceides lepida* Carpine & Grasshoff, 1975 (Fig. 1.1F). Four established common species from Antipatharia order are: *Leiopathes glaberrima* (Esper, 1792) (Fig. 1.1I), *Antipathes dichotoma* Pallas, 1766 (Fig. 1.1H), *Parantipathes larix* (Esper, 1788) and *Antipathella subpinnata* (Ellis and Solander, 1786).

In the Mediterranean, CWCs can be found in a variety of habitats, however, it is often referred to continental shelf and slope, seamounts and submarine canyons as areas of high CWC presence, biodiversity and density.

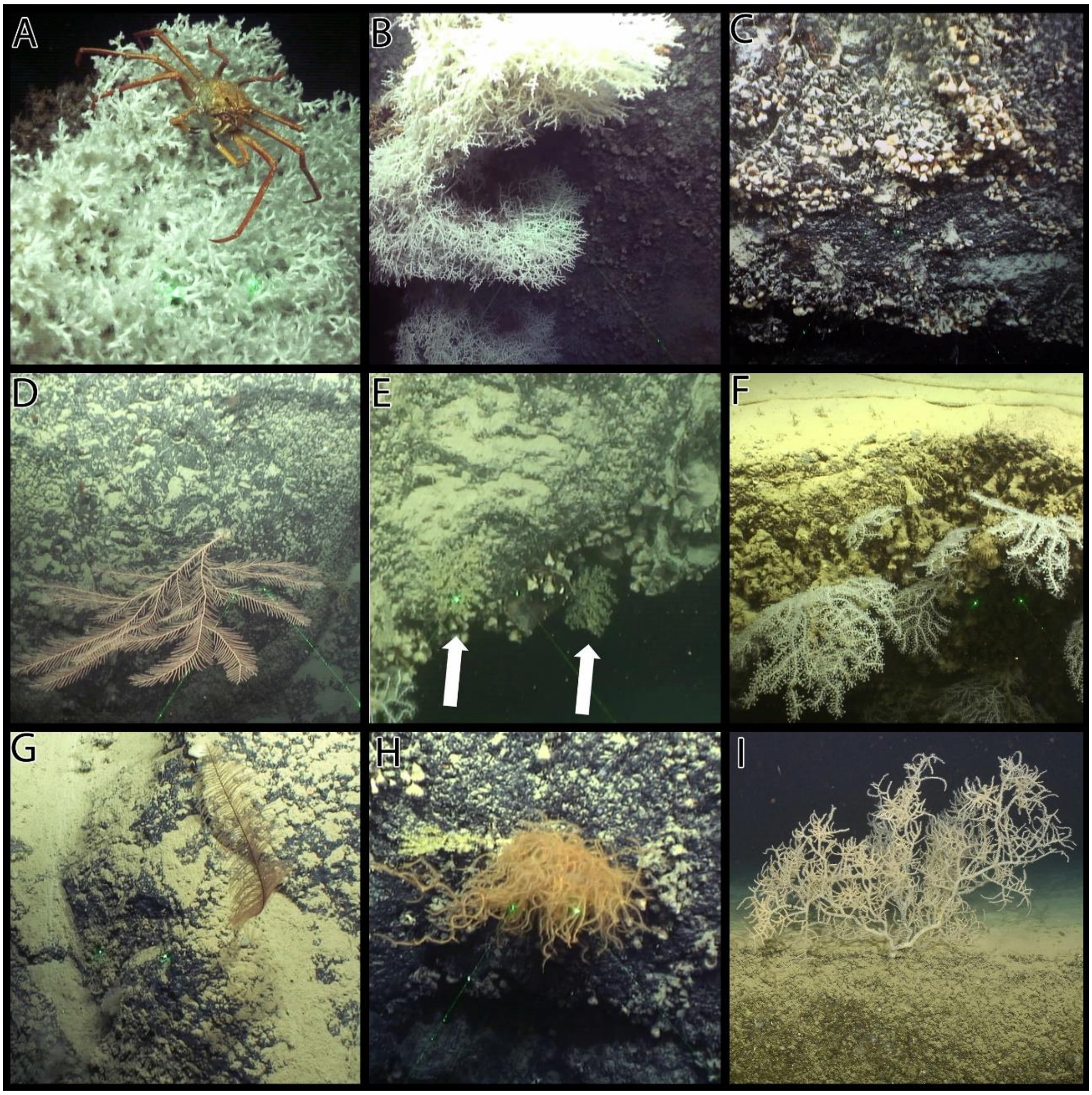


Figure 1.1 Main coral species studied in this thesis: *Desmophyllum pertusum* (A); *Madrepora oculata* (B); *Desmophyllum dianthus* (C); *Callogorgia verticillata* (D); *Acanthogorgia hirsuta* (E); *Muriceides lepida* (F); *Paratipathes* cf. *tetrasticha* (G); *Antipathes dichotoma* (H); *Leiopathes glaberrima* (I). Distance between lasers is 10 cm.

1.3.CWC in submarine canyons

A global overview of geomorphic features stated that the Mediterranean and Black Seas host together 817 canyons (8.6% of all canyons) which belong to the shortest canyons (mean length is 26.6 km) with the smallest incision depth (1093 m) and smallest mean area (200 km^2) (Harris et al., 2014). Particle fluxes channelled from shallow waters into submarine canyons can be several orders of magnitude higher than on the open slope

(Palanques et al., 2005; Zúñiga et al., 2009; Puig et al., 2014). As a result, canyons are important conduits of material from the continental shelf to the deep sea, including sediment, organic matter and pollutants. Submarine canyons also have an important effect on local hydrodynamics as they intercept and deflect density fronts and slope currents, thus enhancing energy exchange between slope and shelf (Palanques et al., 2005; Allen and Durrieu de Madron, 2009; Canals et al., 2013; Fernandez-Arcaya et al., 2017). Hydrodynamics within the canyon can be complex, including an interplay of tidal effects, internal waves, upwelling and downwelling. Generally, the bottom current is aligned with the canyon axis, adjusting to the canyon topography (Puig et al., 2000). This can cause complex vertical motions that can lead to upwelling of nutrients-rich waters and resuspension of the soft sediment on the canyon axis (Ryan et al., 2005). On the other hand, downwelling helps trap particles, thus increasing particle fluxes within the canyon. Moreover, internal waves are frequent events as a product of different current regimes found at the surface and within the canyon, divided by density fronts (Palanques et al., 2005). Atmospheric forcing can have significant effects on sediment and water column dynamics, such as in case of severe storms and strong winds, again enhancing the exchange between the shelf and slope via submarine canyons (Sanchez-Vidal et al., 2012). Moreover, canyons can include a number of intense hydrodynamic phenomena, such as dense shelf water cascading (DSWC), a process that starts with densification of surface water through cooling and evaporation, causing its sinking to larger depths (Canals et al., 2006; Puig et al., 2008; Canals et al., 2009; Puig et al., 2014). Once reaching the shelf break, the dense water cascades down into the canyons, bringing large volumes of sediment and other surface particles with it, as well as living organisms (Palanques et al., 2006a; Arjona-Camas et al., 2021).

The dynamic and variable conditions in submarine canyons are also reflected in the biodiversity they host (Würtz, 2012). Close to the canyons, primary productivity can be enhanced as upwelling brings nutrients to the surface, which further increases phytoplankton and zooplankton communities that attract pelagic and benthic consumers (Ryan et al., 2005; Moors-Murphy, 2014; Almeida et al., 2018; Santora et al., 2018). Soft bottom detritivore communities can be found mostly in the canyon axis due to increased sedimentation rate, where they are important components of this ecosystem as they process the organic matter stored in the sediment (Romano et al., 2013; Román et al., 2016, 2018). Moreover, within the canyons it is common to find bottom and intermediate nepheloid layers which have a higher suspended sediment concentration than the surrounding environment (Puig and Palanques, 1998). This is an important feature for a variety of species, such as larvae of fish and shrimp (Puig et al., 2001; Fernandez-Arcaya et al., 2013), and is likely important for suspension feeders such as CWCs and sponges, living on the rocky canyon walls. Lastly, spatial heterogeneity of submarine canyons is considered fundamental driver of high biodiversity, labelling submarine canyons as biodiversity hotspots (De Leo et al., 2010; McClain and Barry, 2010; Huvenne et al., 2011; De Leo and Puig, 2018; Pearman et al., 2023).

Since submarine canyons are often found close to the coastline, they are prone to experiencing the effects of different anthropogenic activities, some of which can have long lasting negative impacts on their communities. These include fishing, fossil fuel extraction, accumulation of pollutants and litter, as well as climate change impacts (Fernandez-Arcaya et al., 2017). For the purpose of this thesis, we will focus on fishing and related litter accumulation.

Fishing activities taking place close to the canyons or on canyon flanks and rims can have several ways of impacting the local ecosystems (e.g., increase in opportunistic species, loss of ecosystem engineers, change in the biogeochemical composition), depending on the fishing method and intensity (Tillin et al., 2006; Maiorano et al., 2022; Tsikopoulou et al., 2022). Longlining is considered to have a lesser impact on benthic species than bottom trawling (Lumsden, 2007; Pham et al., 2014; Brewin et al., 2021; De la Torriente Diez et al., 2022). However, the fishing lines can get entangled in areas of high rugosity, such as canyon walls and outcrops, as well as on benthic species of high morphological complexity such as CWCs (Muñoz et al., 2011; Sampaio et al., 2012; Hernandez et al., 2022). Some of these lines are then abandoned on the organisms, compromising their growth and survival. When entangled lines are recovered, they may completely remove CWC colonies, or cause their detachment and transport down the canyon (Hernandez et al., 2022).

Bottom trawling is recognized as one of the most extensive causes of seabed change, as the heavy doors are dragged through the seabed, maintaining the net open to collect the species of interest (Puig et al., 2012; Martín et al., 2014b; Clark et al., 2016; Amoroso et al., 2018; Kroodsma et al., 2018; Victorero et al., 2018). The major characteristic of this fishing practice is its unselective character, which often results in high quantities of bycatch, depletion of fishing stocks and severe damage to benthic communities (Kelleher, 2005; Clark et al., 2016; Hiddink et al., 2017; Rijnsdorp et al., 2018; Clark et al., 2019). Apart from direct impact, indirect impact of bottom trawling in form of resuspended sediment has been exceptionally researched in submarine canyons, mainly due to their capacity of enhanced particle flux and increased sedimentation rate (Martín et al., 2014c; Paradis et al., 2018; Arjona-Camas et al., 2019; Haalboom et al., 2021). When fishing is taking place on the canyon flanks and rims over soft sediment, the trawlers move this sediment on each side of the heavy doors, leaving a long strip of displaced compacted sediment (Puig et al., 2012). This can eventually cause turbidity currents characterized by high sediment concentrations and high speeds, also known as sediment gravity flows (Puig et al. 2014a). At the same time, as the trawlers are moving, a part of the sediment is resuspended in the water column, where fine grains can stay in suspension for a long time (up to several days) and travel long distances (hundreds of meters) as enhanced nepheloid layers(Palanques et al., 2001; Durrieu De Madron et al., 2005; Martín et al., 2014b). Measurements done in canyons, showed bottom trawling causing daily turbidity peaks that have the highest concentration close the bottom, and progressively diminish towards the surface during several hundreds of meters (Martín et al., 2014a, 2014c).

The increased need for understanding anthropogenic impacts in the deep sea, alongside technological advancements that support visual based exploration have increased global interest for the deep sea and the need for meaningful spatial management (Elsler et al., 2022; Gaill et al., 2022; Levin et al., 2022). Consequently, several conservation initiatives have been set in motion aiming at protecting important habitats and ecosystems that host high biodiversity; are important for specific life stages of species; are vulnerable to anthropogenic impacts, host specific species that are considered endangered, declining or rare (CBD, 2008; OSPAR, 2008, 2010; FAO, 2020; ICES, 2021, 2022). Submarine canyons in the NW Mediterranean meet the criteria for ecologically or biologically significant marine areas (EBSA) (CBD, 2014) and VME (FAO, 2016) as they fulfil several of these conditions. Only 10.3 % of canyons located within Exclusive Economic Zones are 100 % protected while, 13.6% is at least 10 % within a Marine Protected Areas (Fernandez-Arcaya et al., 2017).

1.4. Study site – Blanes Canyon

Blanes Canyon is located in the NW Mediterranean Sea on the Catalan margin (Canals et al., 2013), being one of the largest canyons on this continental margin (Fig.1.1). It is oriented mainly in the N-S direction, its head is located is only at 4 km from the coastline, the depth range is from 70 to 2600 m depth, the incision length is 16.2 km, and the total length is 184 km (Canals et al., 2013). The hydrodynamics of Blanes Canyon is governed by several processes which are variable in space, time and intensity. Firstly, the density front between surface and intermediate waters maintains the flow over the canyon in the first 50 m depth, unbothered by the canyon topography (Ardhuin et al., 1999). Simulations and field measurements indicate that the Blanes Canyon intercepts the Northern Current (NC) which flows from the Ligurian Sea westwards following the continental margin (Ahumada-Sempoal et al., 2013). The NC is extremely important as it essentially mobilizes the local water masses, more specifically the surface modified Atlantic Water (mAW), the seasonal Western Intermediate Water (WIW), the intermediate Levantine Intermediate Water (LIW) and the deep -Western Mediterranean Deep Water (WMDW) (Millot, 1999).

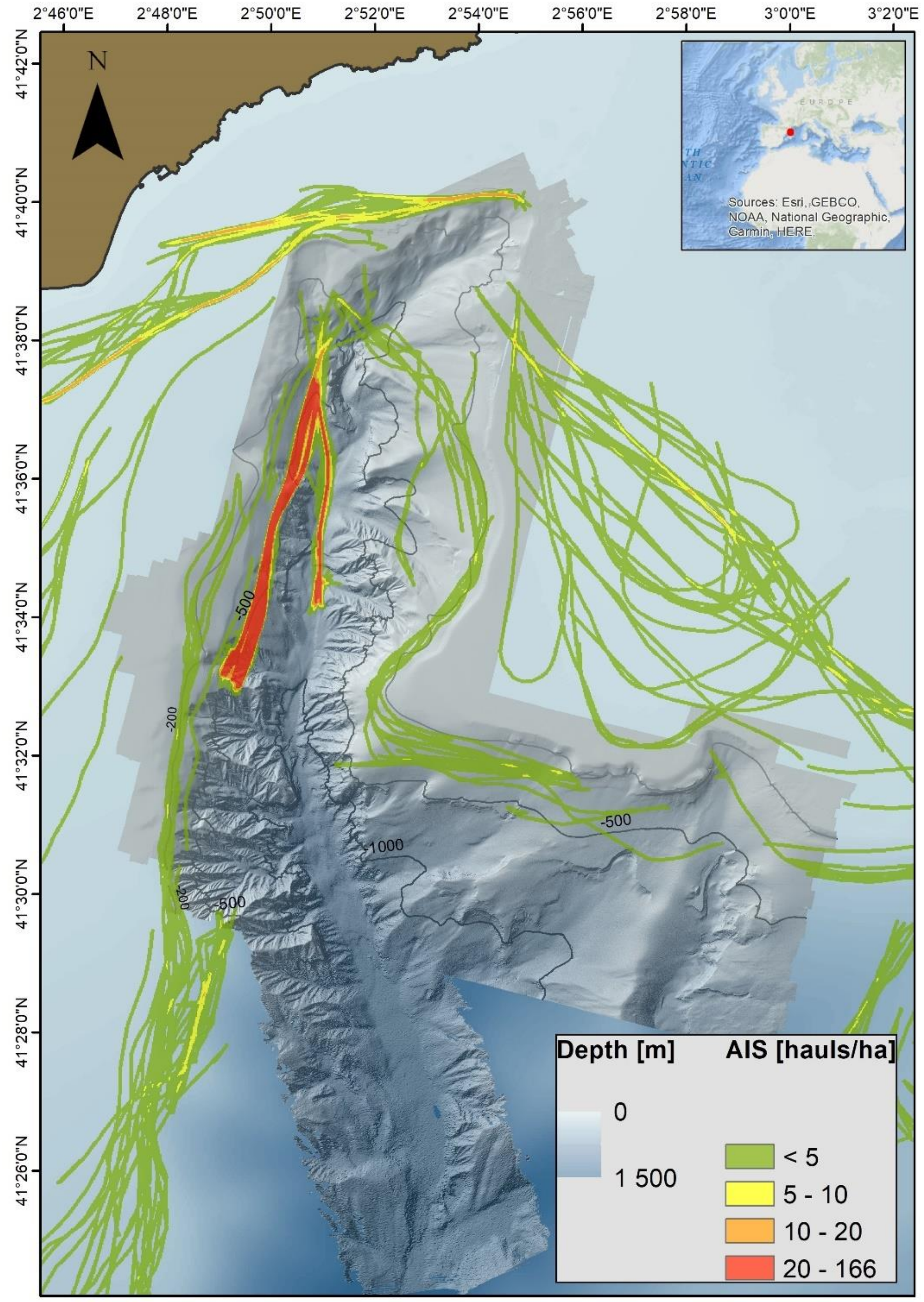


Figure 1.2. Blanes Canyon located in the NW Mediterranean Sea showing main fishing grounds based on Automatic Identification System (AIS) data from 2018 (data provided by Sarah Paradis).

In Blanes Canyon, the NC current creates eddies and meanders resulting in complex water movements that ultimately influence the intensity and frequency of upwelling/downwelling events within the canyon (Flexas et al., 2008; Ahumada-Sempoal et al., 2013). Blanes Canyon occasionally experiences DSWC, especially from nearby shelf (La Planassa) or from water in transit from the Gulf of Lions (Ulses et al., 2008).

This is an important process in the NW Mediterranean as it produces new intermediate water and contributes to formation and ventilation of deep water and causes sediment displacement from the continental shelf to deep sea (see section 1.3.).

Canyon topography enhances particle transport downward, from the continental shelf to the canyon (Granata et al., 1999; Zúñiga et al., 2009), where downward particle fluxes can be up to three orders of magnitude higher than in the open slope (Zúñiga et al., 2009; Lopez-Fernandez et al., 2013b). Moreover, the western flank has more erosional nature due to the southward flow of the current which causes higher particle flux, while the eastern flank is more depositional and characterized by hemipelagic sedimentation processes (Zúñiga et al., 2009; Lastras et al., 2011). The particle fluxes can be highly modified by high energy events such as strong storms or DSWC (Sanchez-Vidal et al., 2012; Durán et al., 2013; Lopez-Fernandez et al., 2013a; Durán et al., 2014). As for other canyons, inputs of material to the Blanes Canyons are not constant, but acting as occasional pulses of sediment and organic matter (Canals et al., 2006; Company et al., 2008; Pusceddu et al., 2010; Lopez-Fernandez et al., 2013a). These dynamic phenomena have an impact on the benthic communities in the canyon, both in the form of physical disturbance but also in terms of food supply and nutrition (Romano et al., 2013; Román et al., 2016).

The continental shelf surrounding Blanes Canyon is divided in La Planassa to the east and Barcelona shelf to the west (Durán et al., 2013). La Planassa shelf is characterized by coarse sediment and rocky outcrops, which is a product of erosion, while Barcelona shelf has evidence of sand deposition (Durán et al., 2013). In cases of severe eastern storms, coarse sediment from the La Planassa shelf is mobilized and deposited in the Blanes Canyon (Sanchez-Vidal et al., 2012; Durán et al., 2013). Moreover, bottom trawling has been identified as a significant contributor to sediment dynamics of Blanes Canyon

(Lopez-Fernandez et al., 2013b; Paradis et al., 2018) (Fig. 1.2). It is especially noticeable during summer months when energetic hydrodynamic forcing, mostly driven by storms and DSWC, are not common, yet particle fluxes in the canyon are high (Lopez-Fernandez et al., 2013b; Paradis et al., 2018). Consequently, the sediment rates along the canyon axis have increased since the 1970s due to technification of the local fishing fleets (Paradis et al., 2018).

Alongside increased sedimentation rates and increased particle flux, increased suspended sediment concentration (SSC) is an inevitable indirect effect of bottom trawling in Blanes Canyon, although not yet directly studied. For the purposes of this thesis, these processes will be considered indirect as they occur adjacent to trawling grounds and have long-lasting effects. However, the scientific community should reconsider the wording as these processes occur along with the direct effects of trawling (e.g., species removal) and are caused by the same, the difference lays in the spatial and temporal components of these processes. They can have specifically important effects on suspension feeding organisms, such as CWCs. So far, ecological studies in Blanes Canyon have highlighted the high species richness and diversity (Atienza et al., 2020). However, most studies have concentrated on commercial species such as crustaceans and fish, or deposit feeders (Sardà et al., 2009; Ramirez-Llodra et al., 2010; Almeida et al., 2018; Román et al., 2018, 2019; Agulló et al., 2020; Carreton et al., 2020). Limited knowledge is available for important habitat forming suspension feeders such as CWCs (Zabala et al., 1993; Aymà et al., 2019; Santín et al., 2020b, 2021a). Zabala et al. (1993) reported several specimens of *D. pertusum* and *M. oculata* collected accidentally by trawling and lobster trammelnet between 180-350 m depth. Following, Aymà et al. (2019) reported on accidental catch of CWCs (*D. dianthus*, *D. pertusum* and *M. oculata*) using Agassiz trawl between 752-1424 m depth along the canyon axis, while ROV observations conducted during that study failed to find CWCs. Finally, Santín et al. (2020, 2021) briefly describe CWCs (*D. dianthus*, *D. pertusum*, *M. oculata*, *P. larix* and *A. hirsuta*) found on canyon walls (ca. 600-860 m) based on ROV observations conducted during ABIDES project. Based on observations found during ABIDES project, ABRIC project was established in order to identify CWC species and their distribution in Blanes Canyon.

1.5. Thesis overview

1.5.1. Research aims

The current thesis aims at characterizing the distribution of megabenthic and CWC communities found on the walls of Blanes Canyon and their hydrographic constrain, and at increasing our understanding of indirect effects of bottom trawling sediment resuspension on the most important habitat forming species.

Chapter 2 describes the megabenthic communities found on the rocky walls of Blanes Canyon based on the data collected during ABRIC 1 cruise that took place in February 2020, funded by Spanish Ministry of Science, and executed by Institut de Ciencies del Mar (ICM-CSIC) in Barcelona.

The main question this chapter addresses is:

Q1 – What are the megabenthic communities found on the walls of Blanes Canyon?

Chapter 3 is dedicated to the description of water column characteristics in Blanes Canyon, more specifically in areas close to CWC presence confirmed in the second chapter. Moreover, this chapter provides a glimpse in the characteristics of a trawling-induced nepheloid layer. Data for this chapter was collected during ABRIC 1 and ABRIC 2 cruises in 2020 and 2021, respectively.

The main question this chapter addresses is:

Q2 – What are the water column characteristics that may affect CWCs in Blanes Canyon and how does bottom trawling modify them?

Chapter 4 adopts an experimental approach to explore the effect of increased SSC, induced by trawling, on survival, growth and metabolism of major CWC species in Blanes Canyon. The experimental work was performed in ICM-CSIC in Barcelona, Spain following the ABRIC 1 cruise in 2020.

The main question this chapter addresses is:

Q3 – What are the effects of increased SSC related to bottom trawling on CWCs living on the walls of Blanes Canyon?

1.5.2. Thesis structure

The thesis structure follows a Paper Thesis format. The chapters are presented as they are in preparation, under revision or submitted to journals. Tables and figures have been numbered accordingly from the beginning of the thesis. Each chapter is summarized below with publication status and authors contributions.

Chapter 2: Hanging gardens of the Blanes Canyon north-western Mediterranean Sea

Bilan M*, Grinyó J, Cabrera C, Gori A, Santín Muriel A, Huvenne VAI, Fabri M-C, Lo Iacono C, Ambroso S, Durán R, Piraino S, Rossi S, Puig P

*Corresponding author

This chapter is currently being revised by the co-authors

Chapter 3: Water column characterization in areas close to cold-water corals of Blanes Canyon and an insight into effects of bottom trawling sediment resuspension

This chapter is in preparation for publication.

Chapter 4: Vulnerability of six cold-water corals to sediment resuspension from bottom trawling fishing

Bilan M* , Gori A, Grinyó J, Biel Cabanelas M, Puigcerver Segarra X, Santín Muriel A 4 , Piraino S, Rossi S, Puig P

*Corresponding author

This chapter is accepted for publication in *Marine Pollution Bulletin*.

2. CHAPTER 2: Hanging gardens of the Blanes Canyon north-western Mediterranean Sea

2.1.Introduction

Submarine canyons are important features incising continental margins and the flanks of some islands (Vetter et al., 2010; Harris and Whiteway, 2011). They are interruptions to the open slope environment, as they change the local current and sediment dynamics, increase spatial heterogeneity and serve as biodiversity hotspots (Palanques et al., 2005; Puig et al., 2014; Fernandez-Arcaya et al., 2017; Appah et al., 2020). Submarine canyons are biodiversity hotspots as the complex interaction of environmental conditions increases the variability and diversity of ecological niches, which are populated by different species (De Leo et al., 2014, 2010). The submarine canyons of the NW Mediterranean have been identified as such in the pioneering works published during the mid-20th century (Pérès and Picard, 1964; Desbruyères et al., 1973; Reyss, 1973).

Cold-water corals (CWC) are nowadays recognized as one the most important habitat-forming species inhabiting submarine canyons (Chimienti et al., 2019; Puig and Gili, 2019). Nonetheless, the presence and extent of their distribution on said environments is increasing yearly at a worldwide scale, as the widespread use of ROV and other technological advancements allow for an ‘easier’ access to challenging environments, such as on canyon walls (Huvenne et al., 2011; Huvenne and Davies, 2014; Robert et al., 2019, 2015). Canyon walls are suitable habitats for CWCs, as high current velocities, food availability and substrate heterogeneity cater to their basic needs for settlement, growth, dispersion and nutrition (Lo Iacono et al., 2018; Puig and Gili, 2019; Robert et al., 2019; Appah et al., 2020; Fabri et al., 2022).

CWCs can form dense mono- or polyspecific species aggregations, which providing shelter, feeding and/or mating grounds for a myriad of associated assemblages including sponges, molluscs, crustaceans, echinoderms and fish (Buhl-Mortensen and Buhl-Mortensen, 2005; Guilloux et al., 2010; Henry and Roberts, 2017; D'Onghia, 2019; Santín et al., 2021a).

In the Mediterranean Sea, there has been a significant increase in knowledge on CWCs, especially in the last 20 years (Tursi et al., 2004; Orejas & Jiménez, 2019). Several important areas of CWCs occurrence were identified, one of which are the submarine canyons of the NW Mediterranean that include canyons found on the Ligurian margin, Gulf of Lions and Catalan margin (Taviani et al., 2005; Gori et al., 2013; Fabri et al., 2014; Lastras et al., 2016; Lo Iacono et al., 2018; Chimienti et al., 2019; Giusti et al., 2019; Ciuffardi et al., 2023; Santín et al., 2020b, 2021a).

The main anthropogenic threat to those canyons is related to fishing activities, mainly bottom trawling (Juan et al., 2007; Coll et al., 2009; Puig et al., 2012; Ramírez-Llodra et al., 2012). Immediate impact caused by bottom trawling is direct or partial removal of organisms, including untargeted species which is mostly restricted to the canyon flanks and rims (Gorelli et al., 2016). Following are lost fishing gears which are either left i*n situ* or transported from shallower parts into the canyons (Giusti et al., 2019; Hernandez et al., 2022). Lastly, growing understanding of indirect impacts of bottom trawling on submarine canyon environments suggest a strong human-induced increase of suspended sediment concentration (SSC), further bringing to higher sedimentation rates in the canyon axis (Arjona-Camas et al., 2021, 2019; Martín et al., 2014a, 2014b; Paradis et al., 2018). All these aspects associated to bottom trawling activities can have negative impacts on CWCs and associated species. Due to current technological limitations, the majority of Mediterranean canyons still need to be mapped at high resolution and knowledge of deep sea assemblage distribution within them still relies on punctual and isolated studies. On the other hand, due to their vulnerability to global change and anthropogenic impacts, there is an urgent need to identify and characterise existing areas of CWC distribution, among other deep sea ecosystems, in order to inform future spatial management plans and address environmental regulation (Elsler et al., 2022; Gaill et al., 2022; Levin et al., 2022).

Sporadic occurrences of CWCs in Blanes Canyon have been previously reported, mainly concerning *D. dianthus*, *D. pertusum* and *M. oculata* (Zabala et al., 1993; Aymà et al., 2019; Santín et al., 2020b, 2021a). The studies obtained samples from trawling (180-350 m), lobster trammel-net (180-350 m), Agassiz trawling (752 – 1424 m) and ROV (670-860 m), however CWC diversity and densities were not quantified until now. This study provides the much-needed knowledge baseline on species richness and spatial distribution of CWCs and associated megabenthic assemblages found on canyon walls of Blanes Canyon. Using a dense grid of ROV video transects along the canyon along with high-resolution bathymetry data, we explored 1) the composition of megabenthic assemblages and the main environmental drivers of their distribution, and 2) coral species variability along the canyon gradients.

2.2. Materials and methods

2.2.1. ROV video surveys

A series of video surveys were performed in Blanes Canyon during the ABRIC 1 cruise in February 2020 on board the R/V Sarmiento de Gamboa equipped with the ROV Liropus (Fig. 2.1). The ROV Liropus was equipped with an HD Kongsberg OE14-502A camera, depth and altimeter sensors, compass, two parallel lasers 10 cm apart, two manipulators, one suction system and two bioboxes. ROV positioning was tracked almost every second with a HiPAP 350P Simrad ultra-short baseline (USBL) acoustic positioning system and recorded using the HYPACK software.

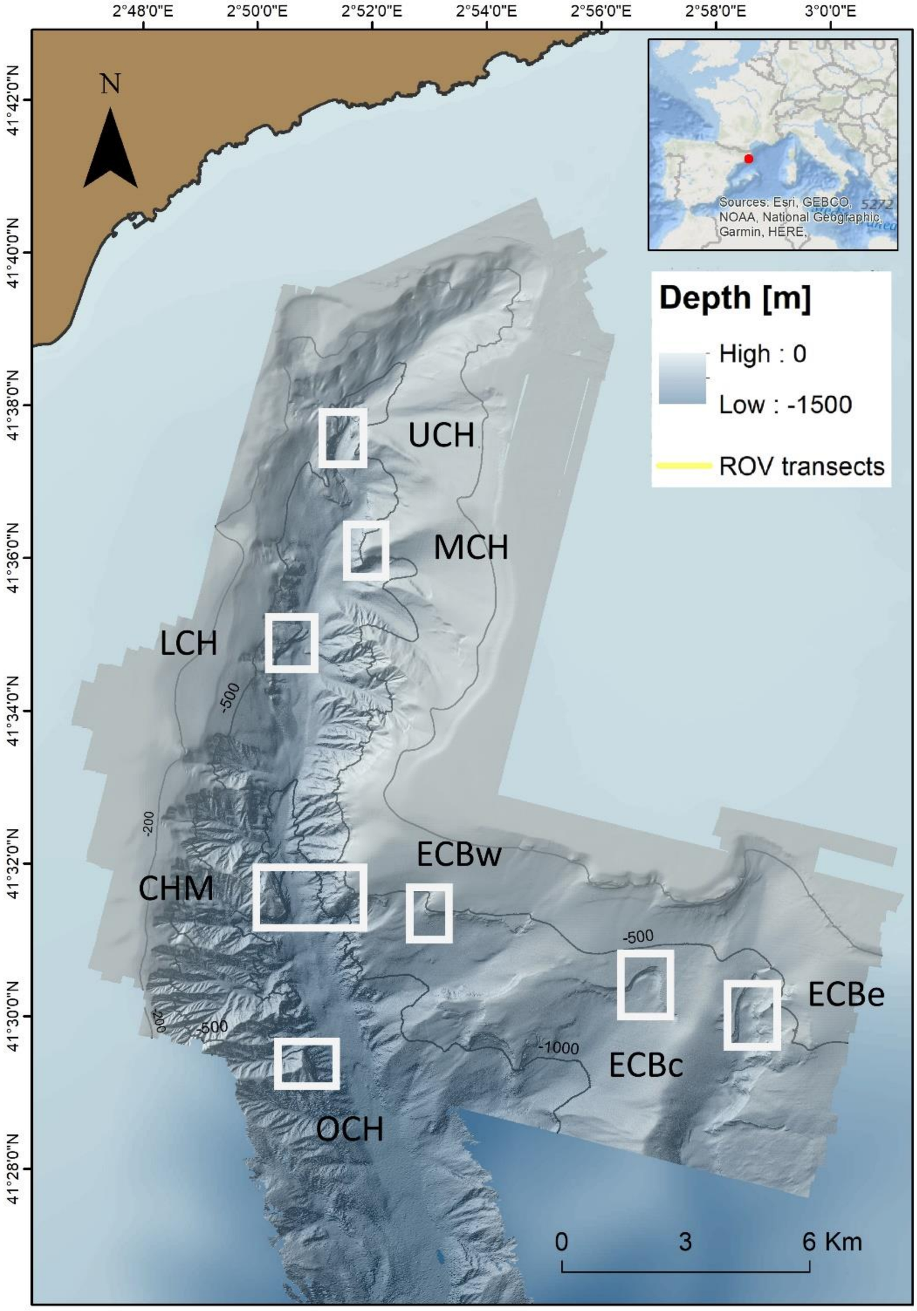


Figure 2.1 Blanes Canyon with 5 m resolution bathymetry using WGS 1984 UTM 31N projection (A). Study sites abbreviated as follows: upper canyon head (UCH) (B); mid canyon head (MCH) (C); lower canyon head (LCH) (D); east canyon branch west (ECBw) (E); east canyon branch central (ECBc) (F); east canyon branch east (ECBe) (G); canyon head mouth (CHM) (H); out of canyon head (OCH) (I).

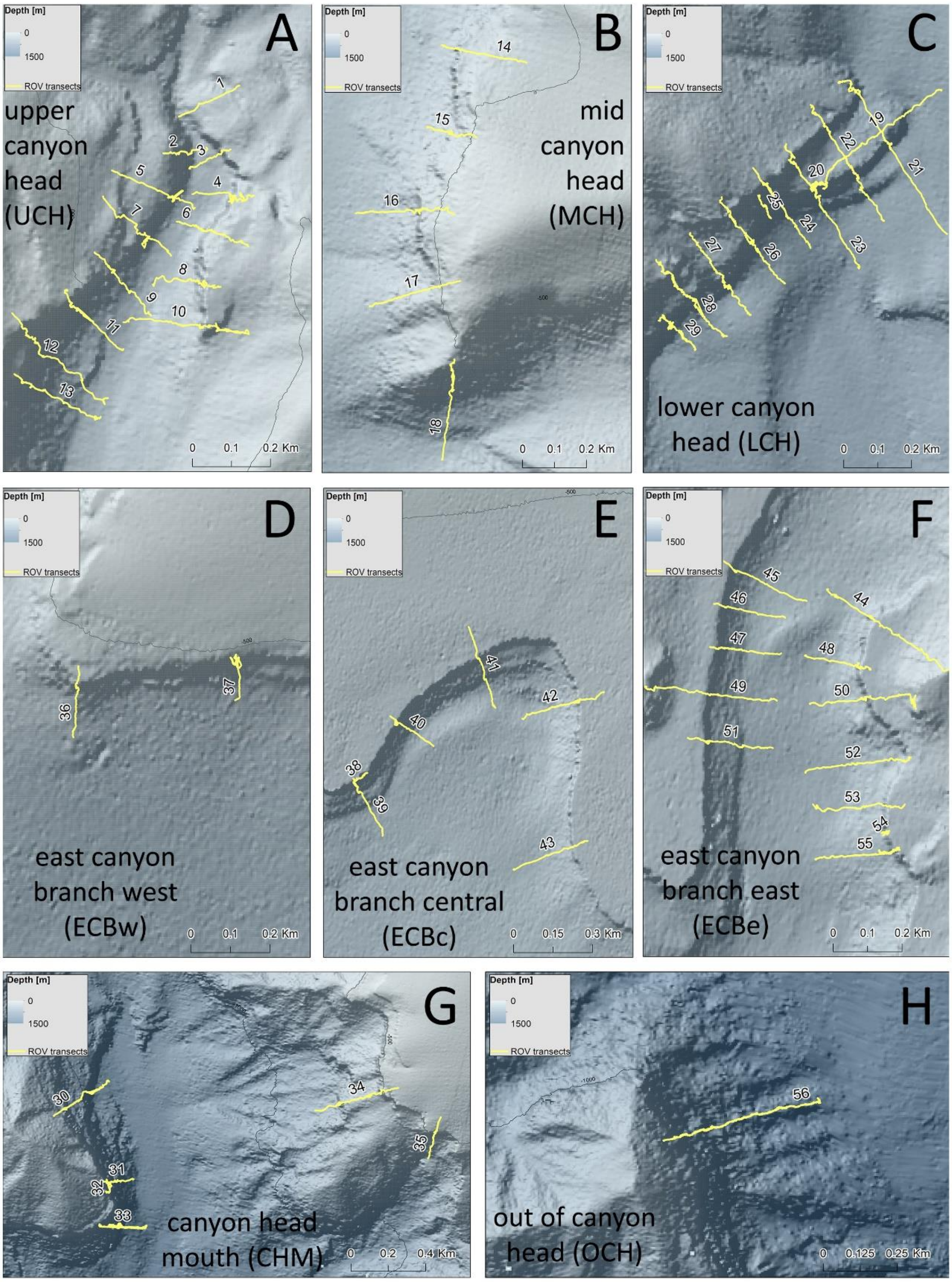


Figure 2.2. Details of Blanes Canyon at study sites: upper canyon head (UCH) (A); mid canyon head (MCH) (B); lower canyon head (LCH) (C); east canyon branch west (ECBw) (D); east canyon branch central (ECBc) (E); east canyon branch east (ECBe) (F); canyon head mouth (CHM) (G); out of canyon head (OCH) (H).

A total of 56 video transects were successfully recorded covering a depth range from 451 to 1305 m depth (Fig. 2.1) (Table 2.1). Survey effort was concentrated in three study sites in the canyon characterized by the presence of steep canyon walls, with the aim of collecting narrowly spaced transects, separated ~100 m among them: upper canyon head (UCH) 13 transects (Fig. 2.2.A), lower canyon head (LCH) 11 transects (Fig. 2.2.C) and eastern canyon branch east (ECBe) 12 transects (Fig. 2.2.F). Additionally, less dense and more spaced video transects were also acquired in other parts of the canyon showing steep terrains: mid canyon head (MCH) 5 transects (Fig. 2.2.B), canyon head mouth (CHM) 6 transects (Fig. 2.2.G), out of canyon head (OCH) 1 transect (Fig. 2.2.H), east canyon branch west (ECBw) 2 transect (Fig. 2.2.D) and east canyon branch central (ECBc) 6 transects (Fig. 2.2.E), to provide a regional view of the CWCs and associated megabenthic assemblages present on canyon walls of Blanes Canyon. All transects started at the bottom of the canyon walls, being the deepest depth of the dive, and continued upwards, over the edge of the wall, until reaching a flat terrain.

Table 2.1. Details on transects performed during ABRIC 1 cruise in Blanes canyon, in upper canyon head (UCH), mid canyon head (MCH), lower canyon head (LCH), canyon head mouth (CHM), east canyon branch (ECB) and out of canyon head (OCH), where latitude and longitude correspond to central point of the transect

Transect number	Study site	Latitude	Longitude	Depth range (m)	Duration	Length (m)
1	UCH	41.632	2.861	576 - 623	37 min	282
2	UCH	41.630	2.860	564 - 628	48 min	306
3	UCH	41.630	2.861	574 - 627	28 min	227
4	UCH	41.629	2.861	544 - 629	58 min	556
5	UCH	41.630	2.859	529 - 633	58 min	455
6	UCH	41.629	2.861	527 - 636	50 min	465
7	UCH	41.629	2.859	524 - 640	53 min	577
8	UCH	41.628	2.860	529 - 645	59 min	564
9	UCH	41.628	2.858	518 - 647	1h 12 min	570
10	UCH	41.627	2.860	529 - 647	1h 31 min	783
11	UCH	41.627	2.857	487 - 651	1h 3 min	483
12	UCH	41.626	2.856	451 - 655	1h 3 min	659
13	UCH	41.625	2.856	481 - 656	1h 17 min	626
14	MCH	41.607	2.865	519 - 657	45 min	434
15	MCH	41.605	2.864	487 - 632	1h 11min	576
16	MCH	41.603	2.862	464 - 697	1h 2 min	782
17	MCH	41.601	2.863	455 - 656	1h 8 min	585
18	MCH	41.598	2.864	515 - 716	1h 22 min	860
19	LCH	41.584	2.847	729 - 866	1h 30 min	928

20	LCH	41.583	2.845	726 - 758	1h 18 min	865
21	LCH	41.584	2.848	784 - 867	1h 23 min	1137
22	LCH	41.583	2.846	748 - 864	1h 23 min	1105
23	LCH	41.582	2.845	679 - 870	1h 27 min	1250
24	LCH	41.582	2.844	653 - 843	1h 2 min	995
25	LCH	41.582	2.843	696 - 770	40 min	488
26	LCH	41.581	2.843	613 - 830	1h 22 min	750
27	LCH	41.580	2.842	662 - 829	1h 3 min	703
28	LCH	41.580	2.840	622 - 828	1h 15 min	851
29	LCH	41.579	2.840	693 - 826	50 min	677
30	CHM	41.529	2.840	749 - 1146	2h 22 min	1935
31	CHM	41.524	2.842	744 - 1168	1h 18 min	1106
32	CHM	41.524	2.842	792 - 820	45 min	647
33	CHM	41.522	2.842	828 - 1190	2h 7 min	1765
34	CHM	41.529	2.857	469 - 874	3h 26 min	2877
35	CHM	41.527	2.862	463 - 717	48 min	584
36	ECBw	41.522	2.883	516 - 610	32 min	313
37	ECBw	41.523	2.888	490 - 591	59 min	547
38	ECBc	41.507	2.941	606 - 613	23 min	216
39	ECBc	41.506	2.941	605 - 704	58 min	528
40	ECBc	41.508	2.943	580 - 654	1h 59 min	1071
41	ECBc	41.510	2.947	547 - 659	49 min	465
42	ECBc	41.509	2.950	570 - 675	1h 24 min	692
43	ECBc	41.504	2.950	616 - 699	56 min	440
44	ECBe	41.502	2.979	538 - 700	1h 52 min	898
45	ECBe	41.504	2.974	621 - 702	54 min	386
46	ECBe	41.503	2.974	626 - 703	43 min	305
47	ECBe	41.502	2.973	630 - 706	49 min	388
48	ECBe	41.502	2.977	633 - 717	1h 20 min	642
49	ECBe	41.501	2.972	568 - 721	59 min	592
50	ECBe	41.501	2.979	571 - 726	2 h 46 min	1772
51	ECBe	41.500	2.973	636 - 734	50 min	502
52	ECBe	41.499	2.978	636 - 745	55 min	492
53	ECBe	41.498	2.978	640 - 751	35 min	492
54	ECBe	41.497	2.979	647 - 687	37 min	360
55	ECBe	41.497	2.978	622 - 755	51 min	738
56	OCH	41.491	2.850	829 - 1305	1h 59 min	3520

2.2.2. Bathymetric survey

Swath bathymetry was acquired during the ABRIC-3 cruise in April-May 2021on board R/V Ramón Margalef, using a hull-mounted Konsgberg-EM710 system. DGPS provided vessel position and a motion reference unit MRU 5+ from Kongsberg provided real-time vessel attitude values. The dataset provides full coverage of the submarine canyon seabed from the canyon head to the middle canyon, down to 1650 m water depth. Multibeam data was complemented with existing data collected from previous surveys in the continental shelf and slope to create a more detailed and accurate representation of the canyon morphology. Post-processing of the multibeam data, including correction for heading, pitch, heave, roll and refraction was conducted using the CARIS HIPS and SIPS Hydrographic Data Processing System©. Tide and SVP corrections were applied and the sounding data were cleaned to remove erroneous soundings. Filtered soundings were gridded into 5-m digital elevation models (DEM) for the canyon head and into 20 m grid for the upper and middle canyon, providing 100% coverage of the swathed seabed. Backscatter strength, originally measured in decibels (dB), represents the amount of energy that is scattered from the seafloor to the transducer. Backscatter data were processed at 10-m grid size for the entire canyon.

2.2.3. Video analysis

Quantitative video analysis applied in this study followed the methodology by Gori et al. (2011) and Grinyó et al. (2018). The ROV transects were analysed in continuity with video annotation performed in Adobe Premiere Pro 2020. A species identification guide was assembled for megafauna above 3 cm and identified to the lowest possible taxonomic level (Appendix A). For some species, where only the phylum level could be identified, descriptive morphospecies names were used. Substrate was categorized based on the CATAMI Classification Scheme with some modifications applied for Blanes Canyon (Althaus et al., 2015). These are: mud (Fig. 2.3A, B) (CATAMI: CAAB 82001016), boulders (Fig. 2.3C) (CATAMI: CAAB 82001003), coral rubble (Fig. 2.3D) (CATAMI:

CAAB 82001009), rocky overhang (Fig. 2.3E) (no CATAMI equivalent), biogenic-covered vertical wall (Fig. 2.3F) (no CATAMI equivalent), bare rock vertical wall (Fig. 2.3G) (CATAMI: CAAB 82001002) and mud-draped vertical wall (Fig. 2.3H) (CATAMI: CAAB 82001002 veneer).

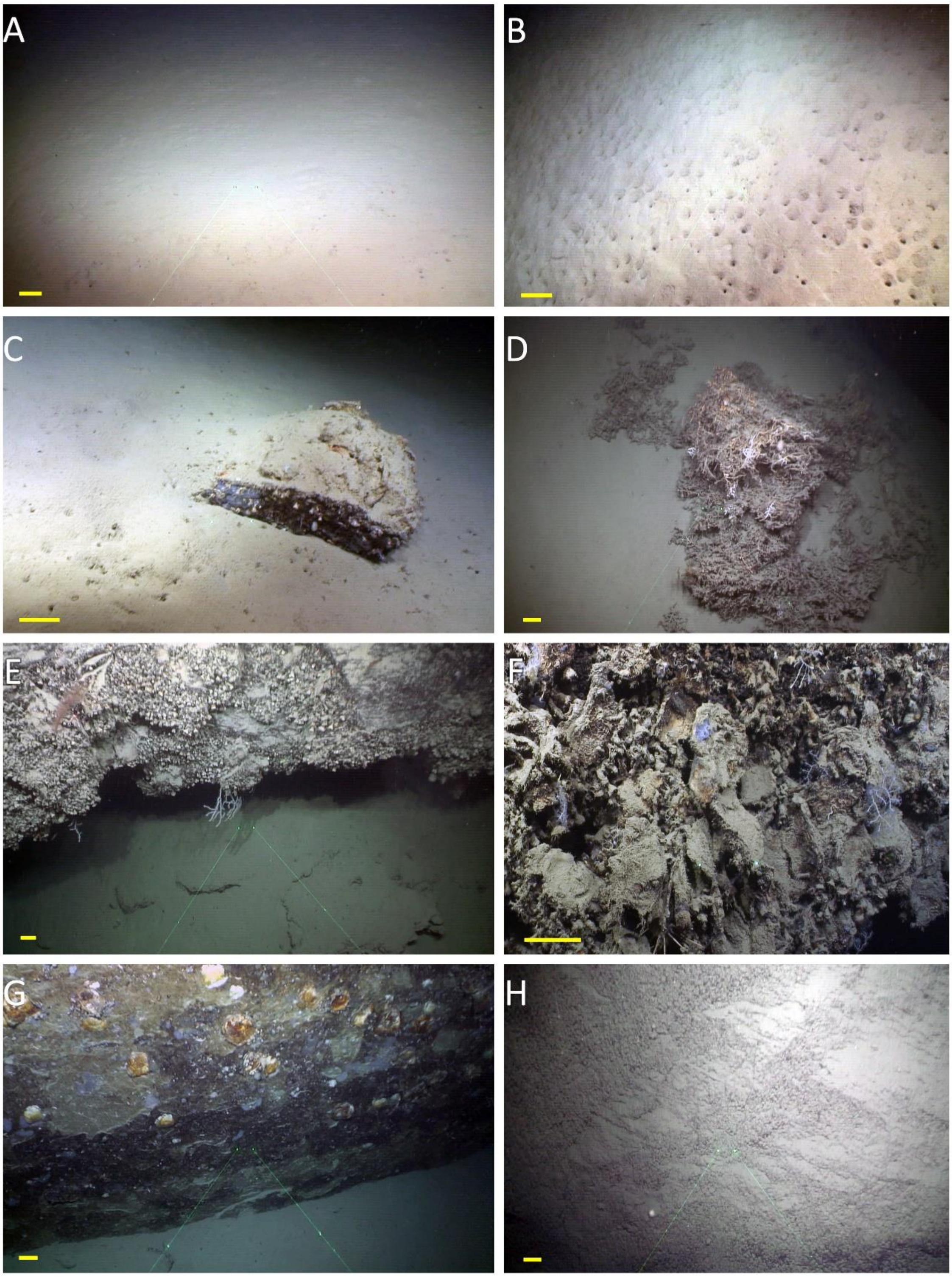


Figure 2.3. Substrate types in Blanes Canyon. Mud (A, B); boulders (C); coral rubble (D); rocky overhang (E); biogenic-covered vertical wall (F); bare rock vertical wall (G); mud-draped vertical wall (H). Scale bars: 10 cm (yellow).

The distinction was made between bare rock vertical wall and mud-draped vertical wall (Fig. 2.3G, H) because large part of the hard substrate was covered with a layer of sediment which led to the question if this thin layer of sediment affects species presence. Video sequence categories were annotated for quality as well if they lasted longer than 3 seconds: good sequence (close to the bottom, uniform velocity, good visibility of the seafloor), parallel (ROV moving sideways), stopped (ROV stopped at bottom or midwater, including sampling) and bad visibility.

Litter was categorized based on the Guidance on Monitoring of Marine Litter in European Seas (European Commission Joint Research Centre Institute for Environment and Sustainability & MSFD Technical Subgroup on Marine Litter, 2013). Litter annotation was done simultaneously with species annotations, where number of items, type of litter and, where applicable, type of interaction with fauna were annotated. Visible trawl marks were also annotated.

Quantitative video analysis consisted of annotating each specimen, litter item or trawl mark seen within 1 m wide section centred on the visible field, established with the software A Ruler for Windows (version 3.4) based on the known distance between the lasers on the ROV (10 cm). Only for *Desmophyllum dianthus* photo grabs were taken to accurately count the individuals in ImageJ since they could reach high densities, and it was difficult to distinguish live and dead corals in constant video annotation. Change in substrate type and video sequence category was also annotated along each video transect.

After removing the outliers from the navigation for each transect in ArcGIS 10.4, gaps in date, time, latitude, longitude and depth were filled in using the *na.fill* function (*zoo* package, Zeileis & Grothendieck, 2005) and *smooth.spline* (*stats* package, embed as part of basic R softaware) in R 4.2.2 (R Core Team, 2022). Distance between each navigation point was calculated using latitude, longitude and depth from which accumulated distance and area were derived based on WGS 1984 UTM Zone 31N projection. Video annotations were combined with navigation data based on date and time, so for each second of the video species and litter abundance was available as numerical value while substrate type and video sequence were categorical values. Based on the accumulated area, 5 m^2 sampling units (SU) were created using the *cut* function in base R (R CoreTeam 2022). Size of the SU was decided since species richness, diversity, and evenness did not differ from larger sampling units (10, 12, 20 and 50 m^2). This size also partially corresponds to bathymetry resolution and similar studies done in the NW Mediterranean used this SU size (Grinyó et al., 2018; Enrichetti et al., 2019; Dominguez-Carrió et al., 2022).

For each SU, based on annotations along the transects, percentage of each substrate type and video sequence category was established, while species and litter abundance were converted to density and only SU that had more than 95% good video sequence were retained for further analysis.

Environmental variables derived from the 5 m multibeam bathymetry resolution are: depth, slope calculated in ArcGIS 10.4, while easteness, northness, planform curvature, profile curvature, total curvature, Terrain Ruggedness Index (TRI) and Vector Ruggedness Measure (VRM) were derived in the spatialECO package (Evans & Murphy, 2021) in R. Backscatter data was provided separately at 10 m resolution. Information from each variable was extracted using the raster package (Hijmans and Van Etten, 2012) in R based on the centroid of each SU. Distance of each SU from canyon tip (2°54´47.55´´E, 41°40´3.69´´N) was also calculated. A correlation matrix was constructed using the variables mentioned and substrate type percentage. All variables that had > 45% correlation were removed from further analysis, leaving with depth, slope, eastness, northness, total curvature (for the bathymetry-derived variables), backscatter, and percentage coral rubble, boulders, biogenic-covered vertical wall, bare rock vertical wall and rocky overhang (for substrate types) (Appendix A).

2.2.4. Data analysis

To identify the major benthic assemblages in the Blanes Canyon, litter, fish, highly mobile crustaceans and molluscs, as well as rare species with less than 5 sightings in the whole study area were removed. Species densities per SU were square root transformed and a Bray-Curtis dissimilarity matrix was generated using the vegan package (Oksanen et al., 2022). Cluster analysis was performed using the *hclust* function in base R with Ward's minimum variance method over the square root transformed dissimilarity matrix (R CoreTeam 2022). Groups were defined based on a 40 % similarity threshold and a PERMANOVA analysis, performed with the *adonis* function from the *vegan* package (Oksanen et al., 2022), was used to establish if they were significantly different. Representative species of each group were identified using the *indval* function from the labdsv package in R (Roberts and Roberts, 2016).

To quantify the effect of retained environmental variables on the distribution of the benthic assemblages, distance-based redundancy analysis (dbRDA) was performed using the *capscale* function from the *vegan* package (Oksanen et al., 2022) that included a square root transformation of the Bray-Curtis dissimilarity matrix.

For each of the study sites, species richness (*S*), Shannon - Wiener diversity index (*H'*) and Pielou evenness index (*J'*) were calculated based on benthic species first, and all species observed, including rare and mobile species, subsequently. Additionally, species accumulation curves and rarefaction curves were constructed for benthic species and all species observed, based on study sites using the *vegan* (Oksanen et al., 2022) and *BiodiversityR* packages (Kindt and Coe, 2005).

2.2.5. Distribution of coral species in the canyon

Geographical distribution and abundance of coral species in the Blanes Canyon was mapped in Arc GIS 10.4 based on SU geographical position, whereas depth, slope and eastness distribution for coral species was visualized using the *ggplot2* package in R (Wickham, 2016).

2.3. Results

A total of 65.6 hours of video material was recorded in the Blanes Canyon during the ABRIC 1 expedition, covering 43,808 m of explored seafloor. The species catalogue consisted of 98 morphospecies and 29 litter categories that were used to identify 46,837 megafauna individuals and 372 litter items during video analysis. Porifera and Chordata were represented by 23 morphospecies each, followed by 22 Cnidaria species, while the other 27 species belonged to Crustacea (12), Echinodermata (8), Mollusca (4) and Annelida (3).

In terms of abundance, 82 % of all observations belonged to Cnidaria, which was mostly driven by *D. dianthus* (20,147 observations), followed by *Muriceides lepida* (445 observations). *Paratipathes* cf. *tetrasticha* was found often along the canyon walls in Blanes Canyon which was surprising as most *Paratipathes* sightings in the Mediterranean belong to *Paratipathes larix* (Marzia Bo, personal communication). Most observations in the phylum Porifera were associated with a small round white porifera (1,255 observations), followed by the encrusting sponge *Hamacantha falcula* (1,031 observations). Chordata had 10 species observed less than 5 times in the whole survey, including *Gaidropsarus granti* and the shark species *Galeus melastomus* and *Hexanchus griseus*, while the most observed Chordata were the ascidian *Dicopia antirrhinum* (311 observations), shortfin spiny eel *Notacanthus bonaparte* (108 observations), common Atlantic grenadier *Nezumia aequalis* (66 observations) and silver roughy *Hoplostethus* *mediterraneus* (64 observations). The most abundant crustacean species were *Munida* sp. (238 observations) and *Plesionika acanthonotus* (71 observations), while the most abundant echinoderm was *Cidaris cidaris* (65 observations). The phylum Mollusca was mostly represented by deep oyster *Neopycnodonte zibrowii* (86 observations), whereas the eurybathic green spoonworm *Bonelia viridis* was the most abundant Annelida (232 observations).

After dividing the transects into 5 m^2 SU there were 8792 SU. Removing those flagged as bad quality, 3,488 SU were left, corresponding to 17,440 m^2. All substrate types were found along the canyon without a clear geographic separation. The most common substrate type was mud (66.2 %), followed by mud-draped vertical wall (24.1 %), coral rubble (3.7 %), biogenic-covered vertical wall (2.2 %), boulders (2 %), bare-rock vertical wall (1.1 %) and rocky overhang (0.3 %).

2.3.1. Megabenthic assemblages

Removal of rare species, highly mobile species and SU without biological data resulted in 1,289 SU for the assemblage analysis. Five significantly different assemblages were identified based on the 40 % similarity threshold (PERMANOVA, p-perm < 0.001) (Fig. 2.4).

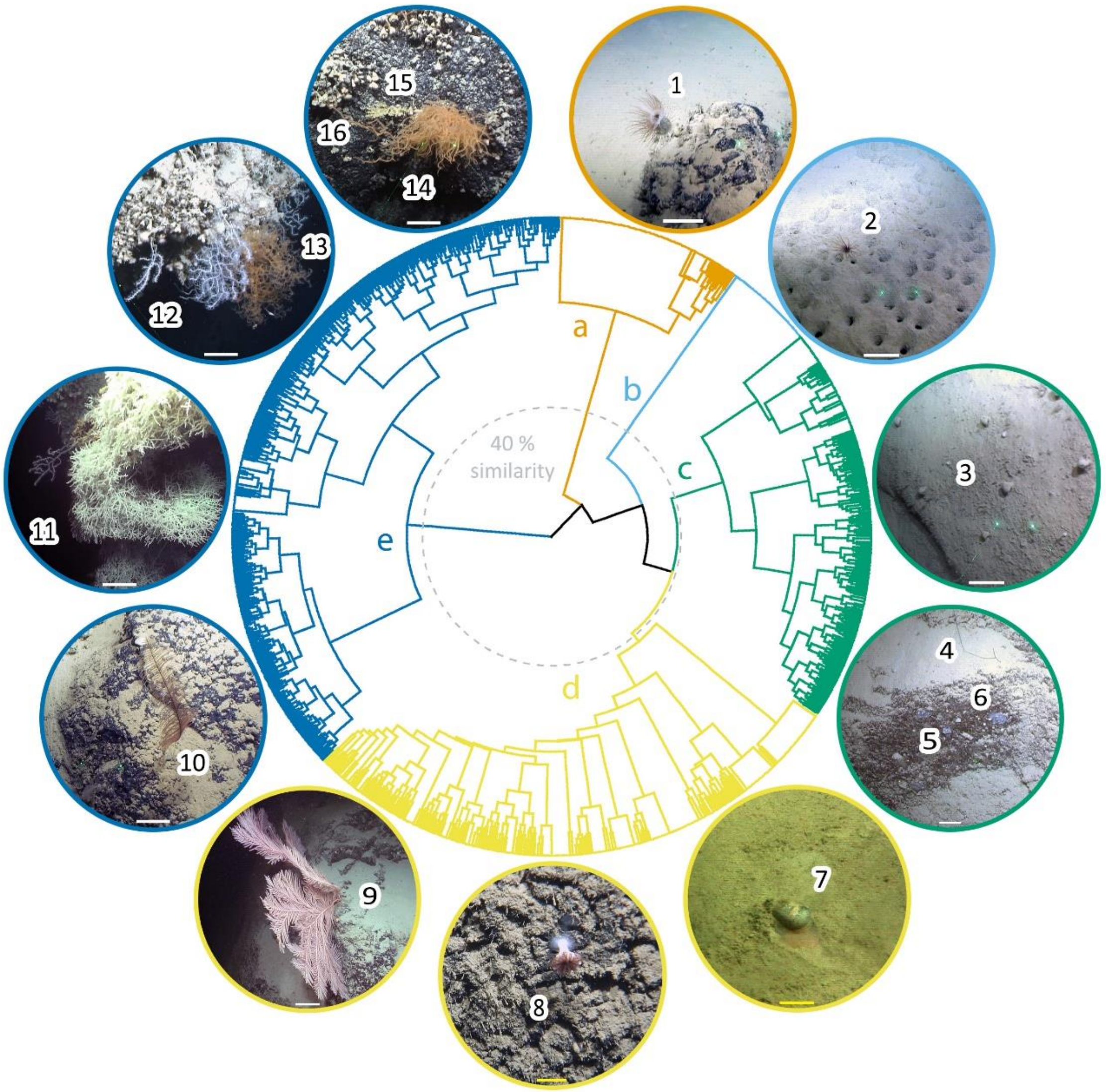


Figure 2.4. Megabenthic assemblages in the Blanes Canyon. Assemblage a: *Cerianthus* sp. (1); Assemblage b: *Arachnanthus* sp. (2); Assemblage c: *Dicopia antirrhinum* (3), *Bonelia viridis* (4), *Hamacantha falcula* (5), Porifera sp.3 (6); Assemblage d: Gastropod (7), *Javania cailleti* (8), *Callogorgia verticillata* (9); Assemblage e: *Parantipathes* cf. *tetrasticha* (10), *Madrepora oculata* (11), *Muriceides lepida* (12), *Leiopathes glaberrima* (13), *Antipathes dichotoma* (14), *Acanthogorgia hirsuta* (15), *Desmophyllum dianthus* (16). Scale bars: 10 cm (white), 1 cm (yellow).

The most representative species per assemblage are shown in Table 2.2 and a brief description of each assemblage follows.

Table 2.2. Summary of characteristic species for each assemblage identified in the Blanes Canyon.

Assemblage	Species	Max. density [org. per m^2]	Mean density ± SD [org. per m^2]	Indicator value

a	*Cerianthus* sp.	1.0	0.2 ± 0.1	0.916
b	*Arachnanthus* sp.	0.2	0.2 ± 0.0	0.953
c	Porifera sp.3	4.0	0.7 ± 0.6	0.583
	Hamacantha falcula	4.0	0.9 ± 0.8	0.278
	Dicopia antirrhinum	1.8	0.4 ± 0.3	0.153
	Bonelia viridis	1.0	0.3 ± 0.1	0.151
	Porifera sp.6	1.4	0.3 ± 0.2	0.138
	Munida sp.	0.8	0.3 ± 0.1	0.091
	Atergia corticata	0.8	0.3 ± 0.2	0.087
d	Gastropod	0.4	0.2 ± 0.0	0.120
	Javania cailleti	2.0	0.7 ± 0.5	0.050
	Callogorgia verticillata	2.8	0.9 ± 0.7	0.049
e	*Desmophyllum dianthus*	107.4	8.2 ± 12.1	0.940
	Madrepora oculata	2.2	0.6 ± 0.4	0.160
	Muriceides lepida	8.8	0.9 ± 1.2	0.140
	Antipathes dichotoma	3.8	0.6 ± 0.6	0.100
	Parantipathes cf. *tetrasticha*	1.4	0.4 ± 0.3	0.070
	Plesionika acanthonotus	0.4	0.2 ± 0.0	0.050

Assemblage a: This assemblage was identified in the 9 % (120) of the analysed SU, usually found bellow or above the canyon wall where mud was the predominant substrate type (Fig. 2.5). To a minor extent, the assemblage was found near coral rubble or on mud-draped vertical walls with average depth at 683 ± 140 m and relatively low slope 21 ± 17° (Fig. 2.5). The assemblage is characterized by a cerianthid from the genus *Cerianthus*, reaching maximum density of 1 ind m^{-2} and average density of 0.2 ind m^{-2} (Fig. 2.4.1 and Table 2.2), found throughout the canyon, usually bellow or above the canyon walls. Additional species in this assemblage were the sea urchin *C. cidaris* and squat lobster from genus *Munida,* usually found on the canyon walls. The crinoid *Leptometra phalangium* was mostly found in the UCH, above the canyon walls.

Assemblage b: This assemblage was characterized by only one species of the genus *Arachnanthus* found throughout the canyon, usually bellow the canyon walls on muddy substrate (Fig. 2.4.2 and Table 2.2). It was identified in 4 % (57) of the analysed SU, most occurrences recorded in ECBe. The mean and maximum density of this species was 0.2 ind m^{-2}, at depth of 706 ± 60 m and 16 ± 16° slope (Fig. 2.5).

Assemblage c: This assemblage was dominated by Porifera and accounts for 20 % (261) of the analysed SU. This assemblage was found throughout the canyon, usually on canyon walls with alternating mud and mud-draped vertical wall at 678 ± 147 m depth and 51 ± 18 ° slope (Fig. 2.5). The most representative of the 24 species forming this assemblage, are an unidentified small, round white sponge (Porifera sp.3) (Fig. 2.4.6) found in 84 % of the SU, with an average density of 0.7 ± 0.6 ind m^{-2}, and the encrusting blue-grey sponge *H. falcula* found in 42 % of the SU, with an average density of 0.9 ± 0.8 ind m^{-2} (Fig. 2.4.5 and Table 2.2). Other important contributors were the ascidian *D. antirrhinum* (Fig. 2.4.3), the spoonworm *B. viridis* (Fig. 2.4.4) and an unidentified sponge Porifera sp.6. Several coral species were found in this assemblage such as *D. dianthus* and *P.* cf. *tetrasticha* but were not significantly representative of the assemblage.

Assemblage d: This assemblage was found in 28 % (364) of the analysed SU, mostly on mud-draped vertical wall (53 %), as well as on mud (32 %) and coral rubble (9 %) (Fig. 2.5). Unlike previous assemblages, assemblage d was mostly observed on east facing slopes (Fig. 2.5). It was the deepest of the identified assemblages, occurring at 778 ± 185 m depth and 43 ± 23° slope. The assemblage is composed of species that are often found in other assemblages (especially c and e) and species that are relatively rare throughout the canyon or only frequent in specific areas. Therefore several species recognized as indicator species have low indicator values, such as an unidentified snail Gastropod (Fig. 2.4.7) with a mean density of 0.20 ± 0.04 ind m^{-2}, found mostly bellow the canyon walls in UCH and ECB; the cup coral *Javania cailleti* (Fig. 2.4.8) with a mean density of 0.7 ± 0.5 ind m^{-2} almost exclusively found on the CHM west wall; and the octocoral *Callogorgia verticillata* with a mean density of 0.9 ± 0.7 col m^{-2}, which was mostly found on the LCH and CHM west wall (Fig. 2.4.9) (Table 2.2). Other species assigned to this assemblage were *Brissopsis lyrifera* sporadically found bellow canyon walls, the octocoral *Swiftia dubia* mostly found on the canyon walls in the LCH and the hexacoral *Desmophyllum pertusum* found on canyon walls of UCH, LCH and CHM west wall.

Assemblage e: This was the most common assemblage, found in the 37 % (487) of the analysed SU with 44 species included in the assemblage analysis. This assemblage was also mostly distributed on east facing canyon walls, where biogenic-covered vertical wall (14 %) and mud-draped vertical wall (65 %) were the main substrates at a mean depth of 738 ± 185 m and 59 ± 17 ° slope (Fig. 2.5). Twelve indicator species were identified, the cup coral *D. dianthus* being the most common species widespread in the canyon with a mean density of 8 ± 12 ind m^{-2} and a maximum density of 107 ind m^{-2} (Fig. 2.4.15 and Table 2). Other widespread species in this assemblage were the octocoral *M. lepida* (0.9 ± 1.2 col m^{-2}) (Fig. 2.4.12) and the black coral *P.* cf. *tetrasticha* (0.4 ± 0.3 col m^{-2}) (Fig. 2.3.10), while the hexacoral *Madrepora oculata* (0.6 ± 0.4 col m^{-2}) (Fig. 2.4.11) and the black coral *Antipathes dichotoma* (0.6 ± 0.6 col m^{-2}) (Fig. 2.4.14) were found along the canyon but absent from the ECB (Table 2). The deep oyster *N. zibrowii* was recorded at maximum density of 4.2 ind m^{-2} on bare rock vertical walls, which were present in the 6 % of the SU (Fig. 2.3G, 2.5).

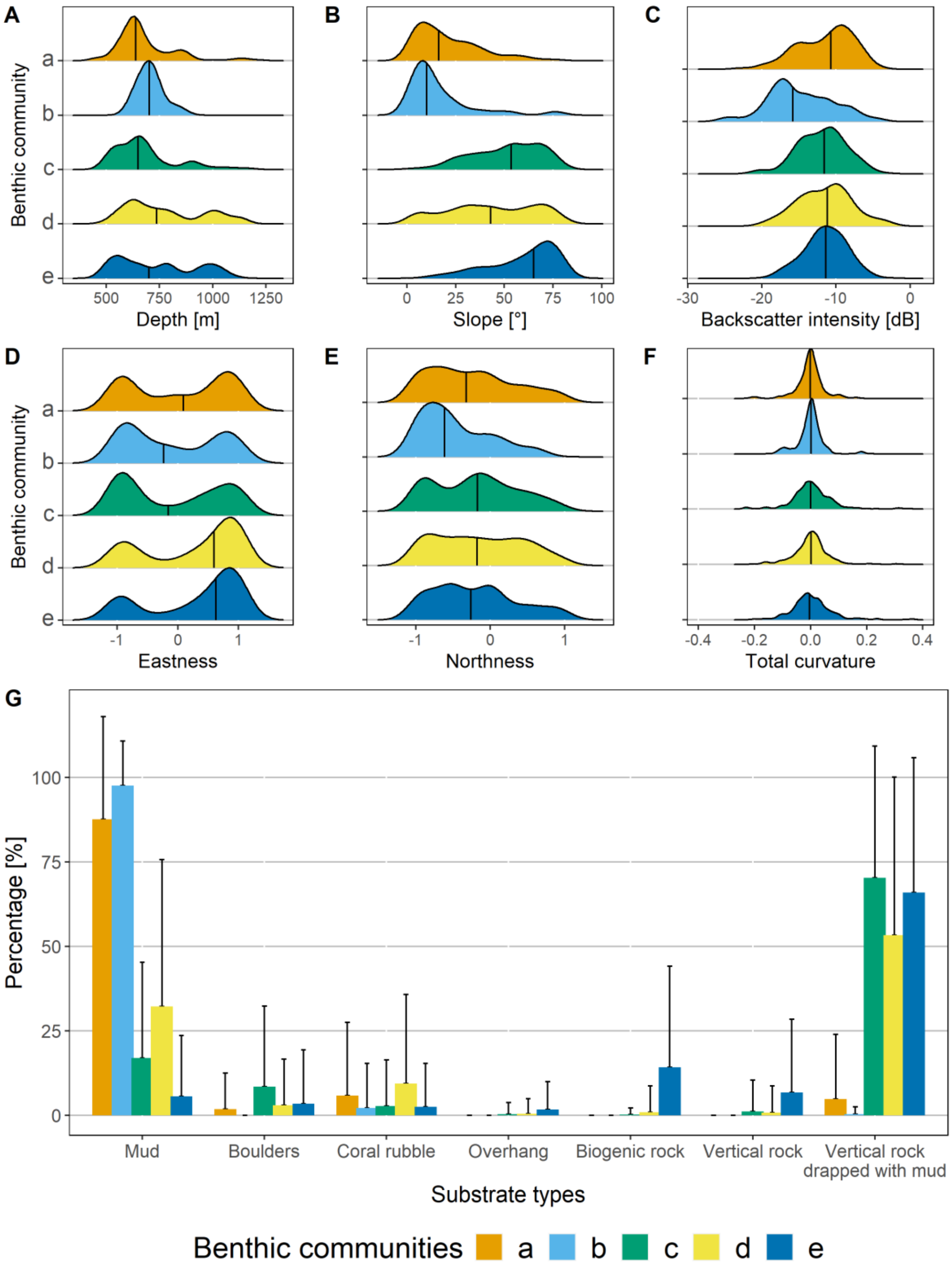


Figure 2.5. Terrain variables and substrate types for identified benthic assemblages in the Blanes Canyon: depth (A), slope (B), backscatter intensity (C), eastness (D), northness (E), total curvature (F) and substrate type (G).

2.3.2. Relation with terrain variables

Distance-based redundancy analysis (dbRDA) showed that the retained terrain variables (Fig. 2.5) explained 10.4 % of all variability observed, with the first two components explaining 74.3 % of constrained variance (Fig. 2.6).

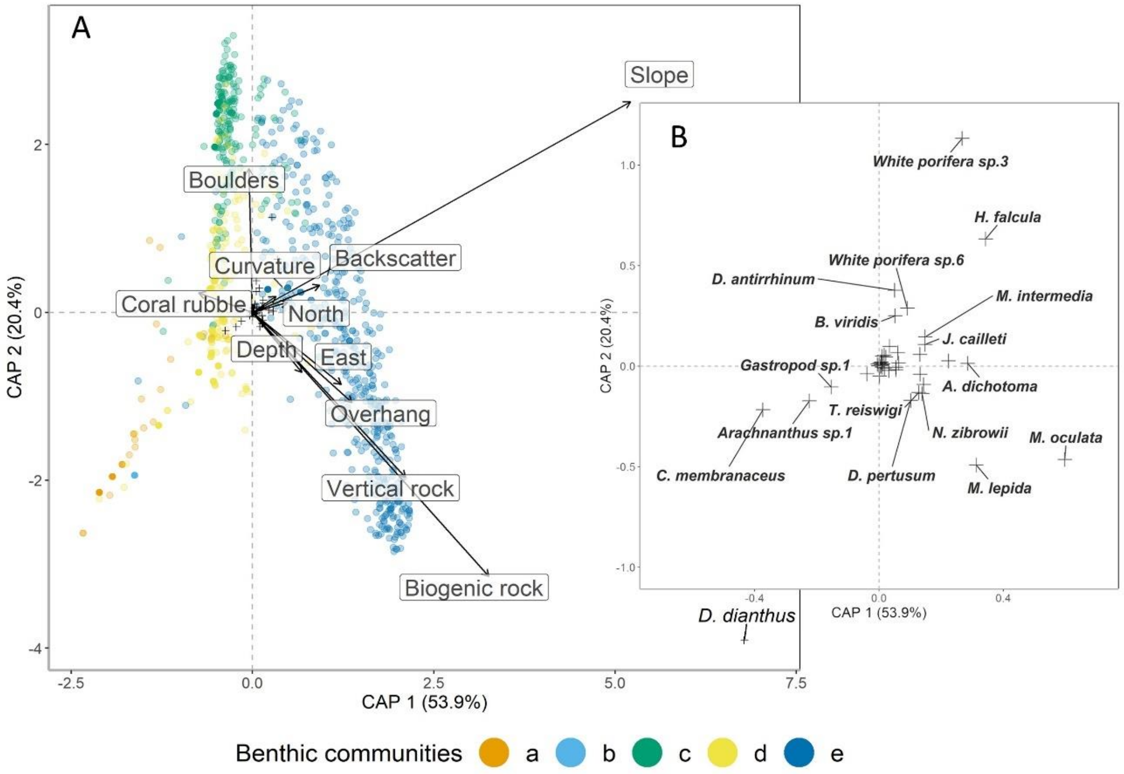


Figure 2.6. Distance based redundancy analysis (dbRDA) based on transformed dissimilarity matrix of SU and density of benthic species constrained with centred terrain variables. Sites scores (coloured dots), terrain variables (arrows) and species scores (crosses) labelling only *D. dianthus* (A); Zoom in the ordination plot with species scores (B).

Permutation test showed that all terrain variables, except for total curvature, significantly improve the model associating biological density of benthic species and terrain variables ($p < 0.001$; 999 permutations) (Table 2.3). The ordination was successful at separating SU and species mostly found on soft sediment (assemblages a and b) from those mostly found on mixed (assemblage c and d) and hard substrate (assemblage e) (Fig. 2.6A). However, since assemblage b was characterized with mud and only one species (*Arachnanthus* sp.), all SU of this assemblage overlap in the ordination plot and are therefore found as one point (Fig. 2.6A). Slope was an important driving force in this study, especially because mud and vertical rock draped with mud were excluded from the analysis for being correlated with slope. Assemblages c, d and e mostly found on rocky walls, while assemblages a and b were found on soft sediment below or above the canyon walls. Coral species and assemblage e dominated on biogenic-covered vertical walls, bare-rock vertical walls and rocky overhangs, especially on east facing flanks (Fig. 2.6A, B). *Desmophyllum dianthus* was an outlier due to its frequency and abundance in the study area. Amidst dead individuals that formed the biogenic-covered rock substrate type as thanatocoenosis together with *N. zibrowii* (Fig. 2.3F, 2.6A), there were often alive individuals.

Table 2.3. Summary of permutation test for distance-based redundancy analysis (dbRDA) of principal constraints.

Variable	Df	SS	F	p
Depth	1	6.97	17.59	< 0.001
Slope	1	24.69	62.34	< 0.001
backscatter	1	2.37	5.98	< 0.001
Eastness	1	1.73	4.36	< 0.001
Northness	1	1.03	2.61	< 0.001
Total curvature	1	0.44	1.11	0.335
Bare-rock vertical wall	1	4.06	1.25	< 0.001
Boulders	1	1.85	4.65	< 0.001
Coral rubble	1	2.55	6.43	< 0.001
Biogenic-covered vertical wall	1	10.42	26.3	< 0.001
Rocky overhang	1	1.71	4.32	< 0.001
Residual	1277	505.68		

2.3.3. Benthic biodiversity of Blanes Canyon

Biodiversity and species assemblages changed throughout the canyon, whereas some species were common to all sites, such as the cup coral *D. dianthus,* Porifera sp.3, and encrusting sponges *H. falcula* and *Hexadella* cf. *dedritifera,* ascidian *D. antirrhinum* and fish *N. bonaparte, H. mediterraneus*, *Hymenocephalus italicus*, *N. aequalis* and *Phycis* *blennoides* (Fig. 2.7, Appendix A). On the other hand, most species showed patchy or site-specific distribution along the canyon, such as *L. glaberrima*, *C. verticillata, Sympagella deluzei, Pachastrella monilifera*, *Poecillastra compressa, N. zibrowii* (Fig. 2.7, Appendix A).

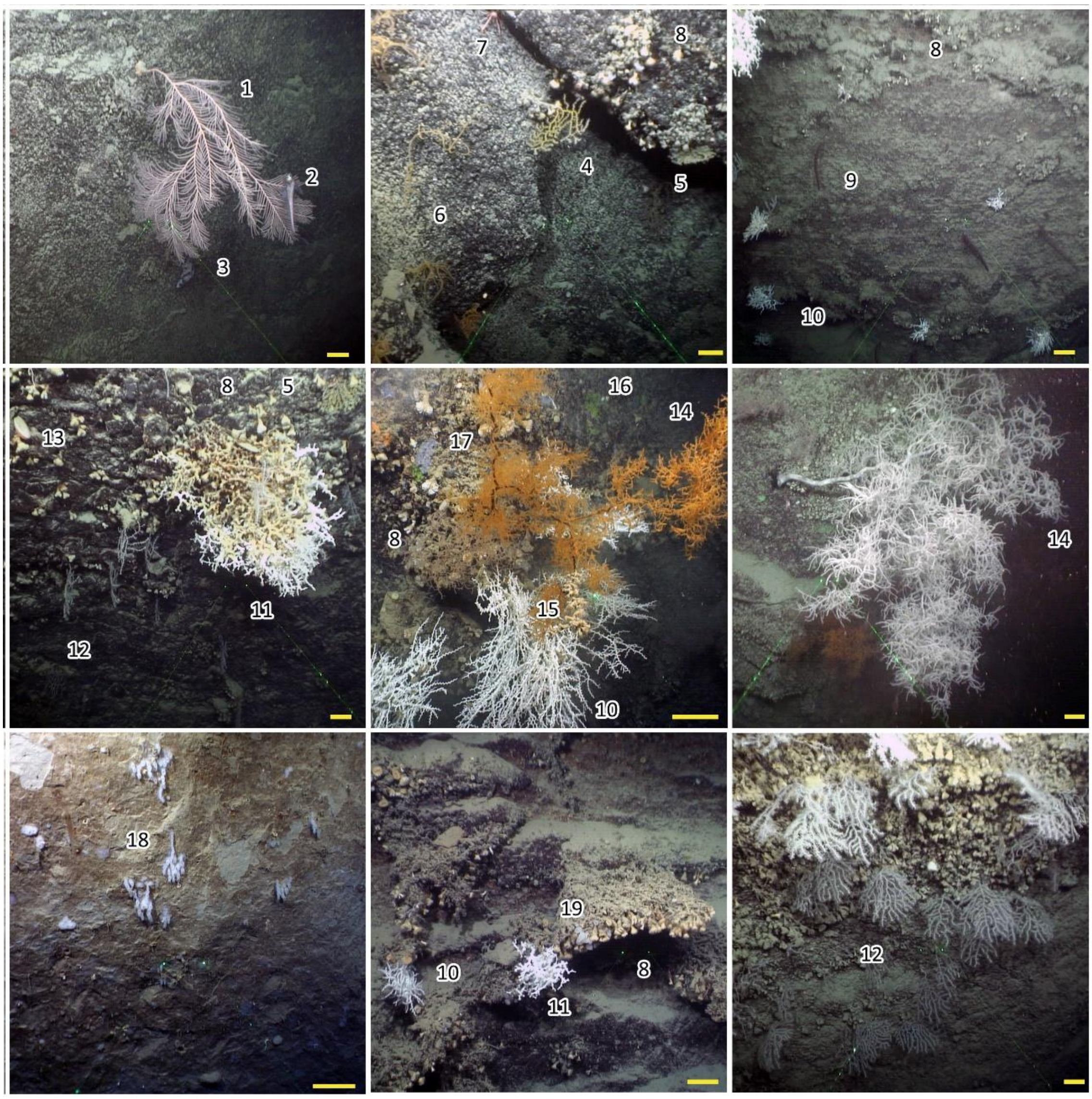


Figure 2.7. Selected species from Blanes canyon walls. *Callogorgia verticillata* (1); *Nezumia aequalis* (2); *Lepidion lepidion* (3); *Placogorgia coronata* (4), *Acanthogorgia hirsuta* (5) *Antipathes dichotoma* (6), *Munida* sp. (7), *Desmophyllum dianthus* (8); *Parantipathes* cf. *tetrasticha* (9); *Madrepora oculata* (10); *Desmophyllum pertusum* (11); *Muriceides lepida* (12); *Acesta excavata* (13); *Leiopathes glaberrima* (14); *Epizoanthus* sp. (15); *Hexadella* cf. *dedritifera* (16); *Hamacantha falcula* (17); *Tretodictyum reiswigi* (18); *Oopsacas minuta* (19). Scale bars: 10 cm (yellow).

Ecological indices and number of SU for each study site are presented in Table 2.4. Highest species richness was found on CHM, benthic (*S*=37) and total (*S*=57), as well as number of SU (Table 2.4). Shannon–Wiener index was recorded highest for ECBw for benthic species (*H'*=1.77) alongside the Pielou evenness index (*J'* = 0.6), while when considering all species ECBc showed the highest Shannon–Wiener index (*H'*= 2.05), and ECBw had the highest Pielou eveness index (*J'*=0.59). Out of canyon head (OCH) showed lowest ecological indices (Table 2.4). The number of SU containing fauna varied considerably between study sites, ranging between 20-339.

Table 2.4. Ecological indices for study areas calculated for benthic species and all species encountered. *S* – species richness, *H'* - Shannon-Wiener diversity index, *J'* - Pielou evenness index, SU – sampling units.

	Benthic species				**All species**			
Study site	***S***	***H'***	***J'***	**SU**	***S***	***H'***	***J'***	**SU**
UCH	35	0.88	0.24	244	54	1.01	0.25	297
MCH	29	1.63	0.48	141	52	1.89	0.47	198
LCH	29	1.53	0.45	181	45	1.81	0.47	247
CHM	37	1.25	0.34	339	57	1.34	0.33	390
ECBw	19	1.77	0.60	20	24	1.87	0.59	22
ECBc	24	1.61	0.50	49	41	2.05	0.55	92
ECBe	33	1.27	0.36	226	54	1.39	0.35	290
OCH	16	0.41	0.14	89	25	0.46	0.14	98

Following the same division as in Table 2.4, species accumulation curves based on SU were visualized using study sites in order to evaluate the effect of variable number of SU between sites (Fig. 2.8A, C). The asymptote was approached after cca. 100 SU at all study sites, with the exception of ECBw and ECBc which had lower SU available (Fig. 2.8A, C, Table 2.4). Rarefaction curves based on individuals counted were similar between sites when considering only benthic species, except for OCH which showed lower values (Fig. 2.8B). When considering all species, several sites emerged, such as MCH, LCH, ECBw (Fig. 2.8D). These sites also had the high values of Pielou eveness index and Shannon-

Wiener diversity index (Table 2.4). In all cases OCH site showed lowest values (Fig. 2.8) (Table 2.4), however only one transect was performed in this area.

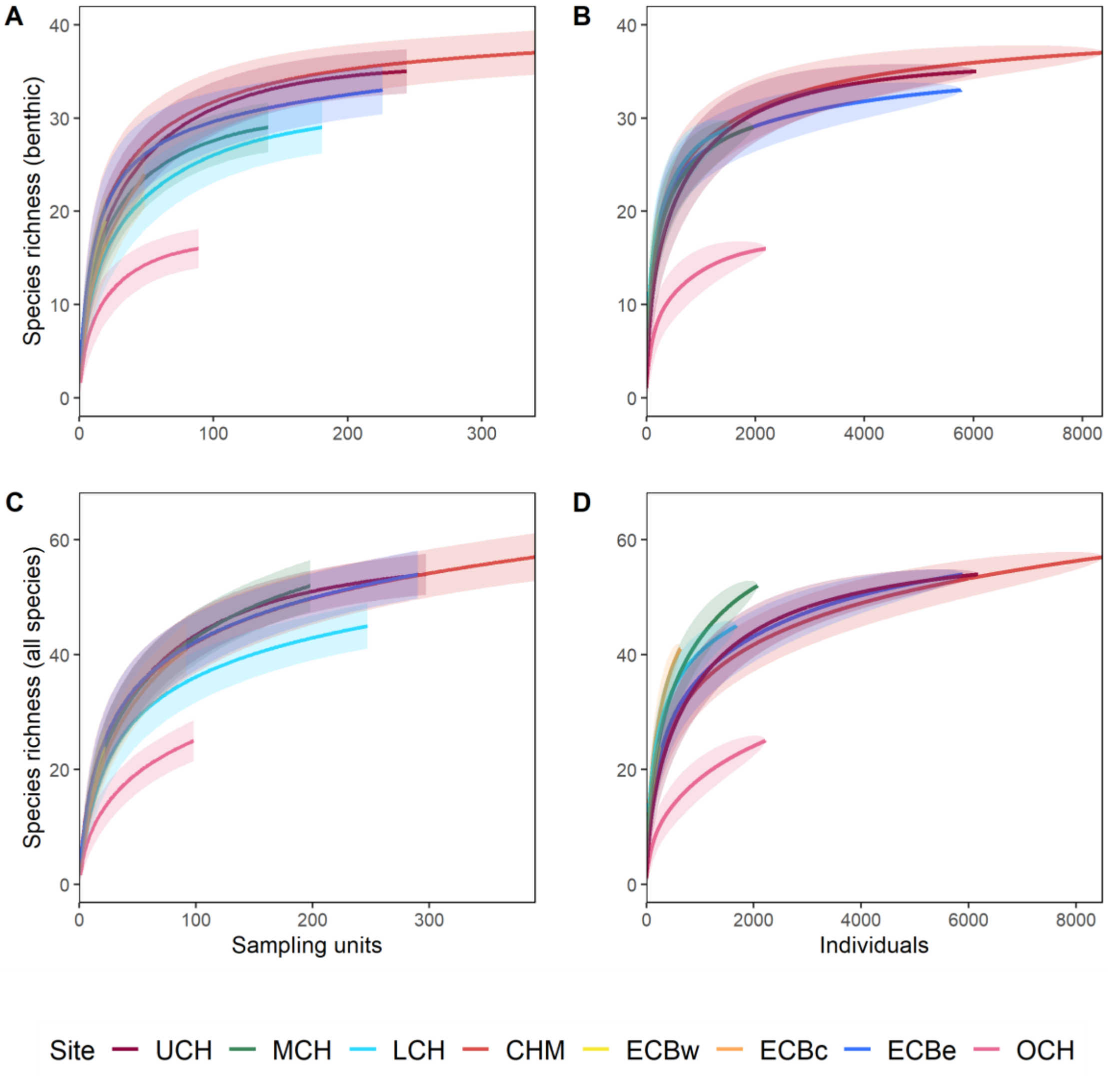


Figure 2.8. Sampling unit-based species accumulation curves for benthic species (A) and all species (C) with individual count rarefaction curves for benthic (B) and all species (D). Shadowed areas corresponding to 95% confidence intervals. Abbreviations: upper canyon head (UCH), mid canyon head (MCH), lower canyon head (LCH), canyon head mouth (CHM), east canyon branch (ECB) and out of canyon head (OCH).

2.3.4. Distribution of the main coral species in the canyon

In Blanes Canyon we identified 12 main coral species (Fig. 2.9). *Desmophyllum dianthus* was the most abundant coral species (Fig. 2.9A), found in all study sites mostly facing downwards. *Muriceides lepida* (Fig. 2.9F) and *P.* cf. *tetrasticha* (Fig. 2.9L) were found in most study sites, where *M. lepida* had highest densities in the ECB and *P.* cf. *tetrasticha* did not reach densities higher than 1.4 col m^{-2}.

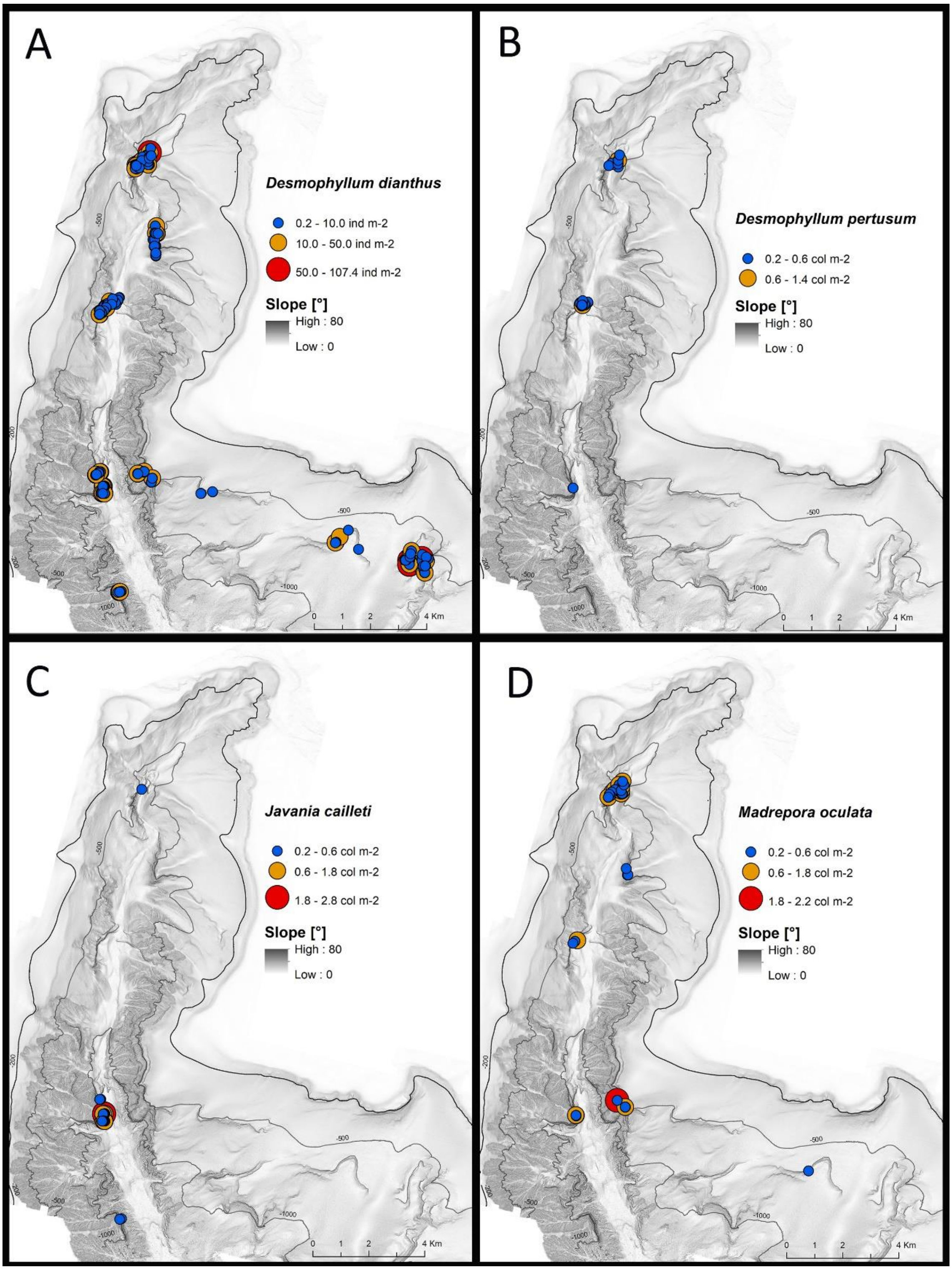


Figure 2.9. Density and distribution of main coral species in Blanes Canyon. *Desmophyllum dianthus* (A); *Desmophyllum pertusum* (B); *Javania cailleti* (C); *Madrepora oculata* (D);

Acanthogorgia hirsuta (E); *Muricides lepida* (F); *Placogorgia coronata* (G); *Swiftia dubia* (H); *Callogorgia verticillata* (I); *Atipathes dichotoma* (J); *Leiopathes glaberrima* (K); *Parantipathes* cf. *tetrasticha* (L).

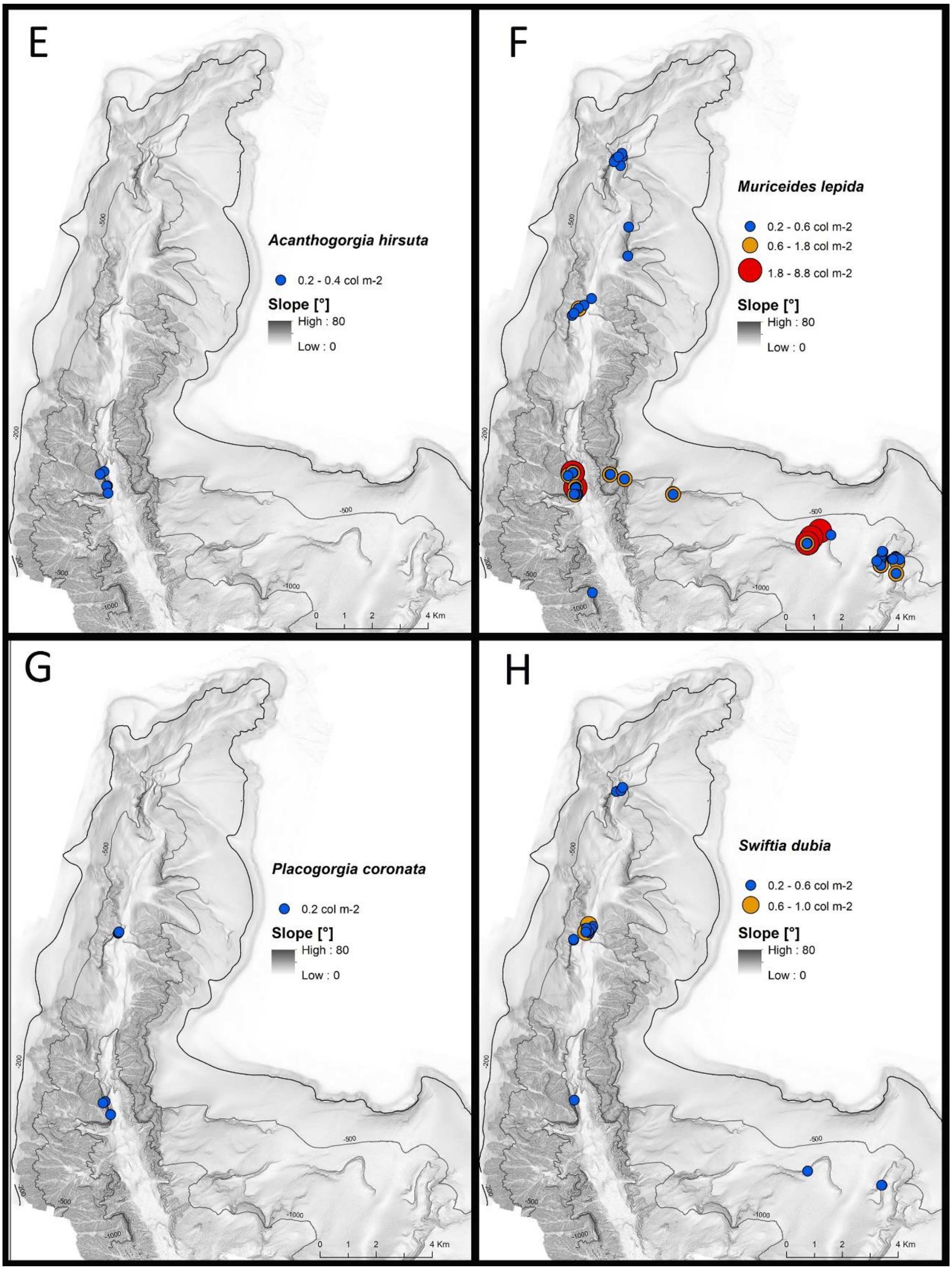


Figure 2.9. (continued) Density and distribution of main coral species in Blanes Canyon. *Desmophyllum dianthus* (A); *Desmophyllum pertusum* (B); *Javania cailleti* (C); *Madrepora oculata* (D); *Acanthogorgia hirsuta* (E); *Muricides lepida* (F); *Placogorgia coronata* (G); *Swiftia dubia* (H); *Callogorgia verticillata* (I); *Atipathes dichotoma* (J); *Leiopathes glaberrima* (K); *Parantipathes* cf. *tetrasticha* (L).

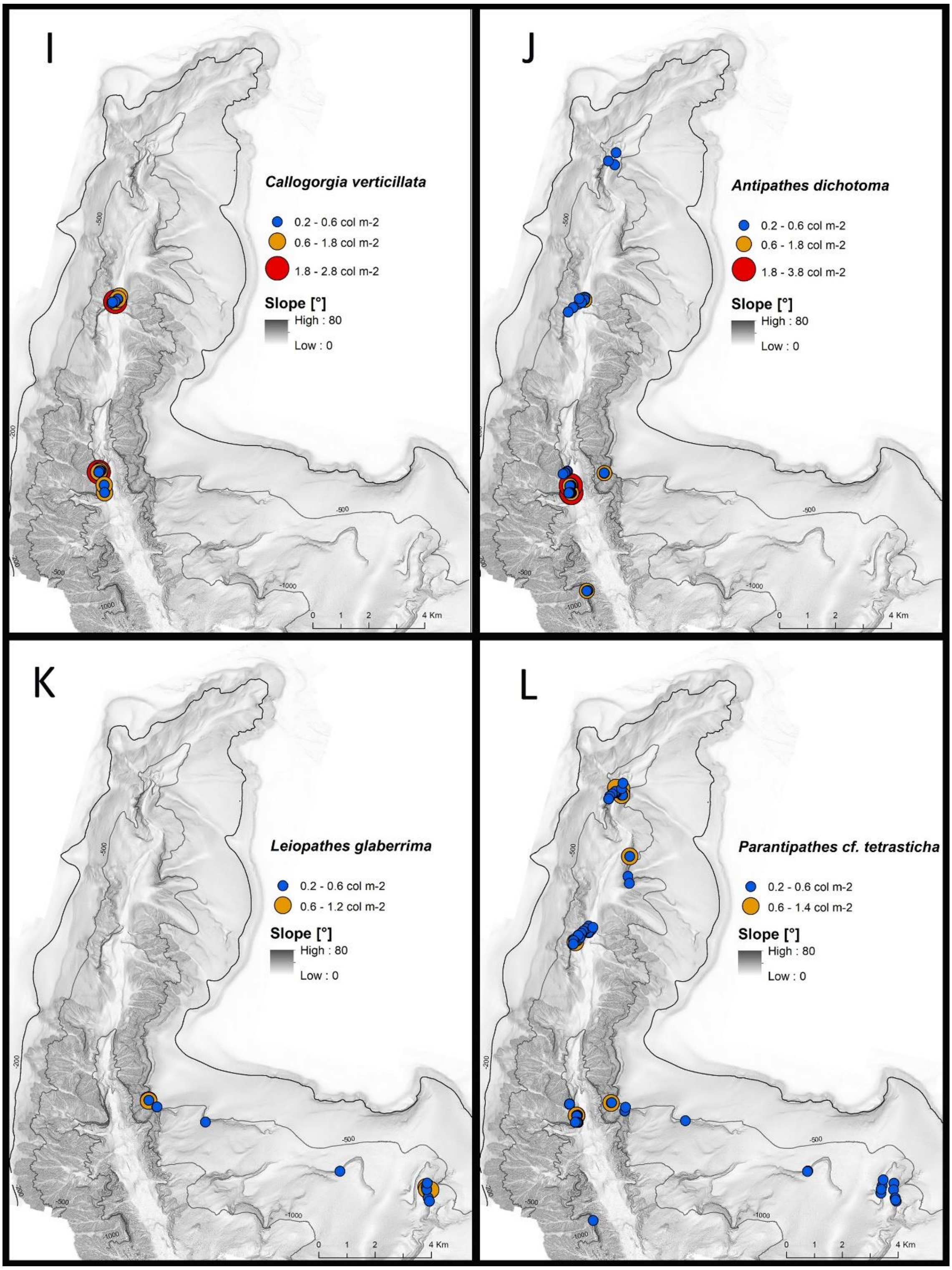


Figure 2.9. (continued) Density and distribution of main coral species in Blanes Canyon. *Desmophyllum dianthus* (A); *Desmophyllum pertusum* (B); *Javania cailleti* (C); *Madrepora oculata* (D); *Acanthogorgia hirsuta* (E); *Muricides lepida* (F); *Placogorgia coronata* (G); *Swiftia dubia* (H); *Callogorgia verticillata* (I); *Atipathes dichotoma* (J); *Leiopathes glaberrima* (K); *Parantipathes* cf. *tetrasticha* (L).

Colonial scleractinian species (*D. pertusum* and *M. oculata*) were mainly found in sites along the canyon head (Fig. 2.9B, C). It is worth noting that qualitative observations on growth patterns and directions differed between sites, where seemingly in most sites, especially UCH, they mostly grew facing downwards as the upper part was covered with sediment (Fig. 2.10A), *D. pertusum* colonies were found in LCH on soft substrate, growing in a cone shape facing the main current (Fig. 2.10B). In CHM, both species were found less covered with sediment and possibly growing upwards as well as downwards (Fig. 2.10C).

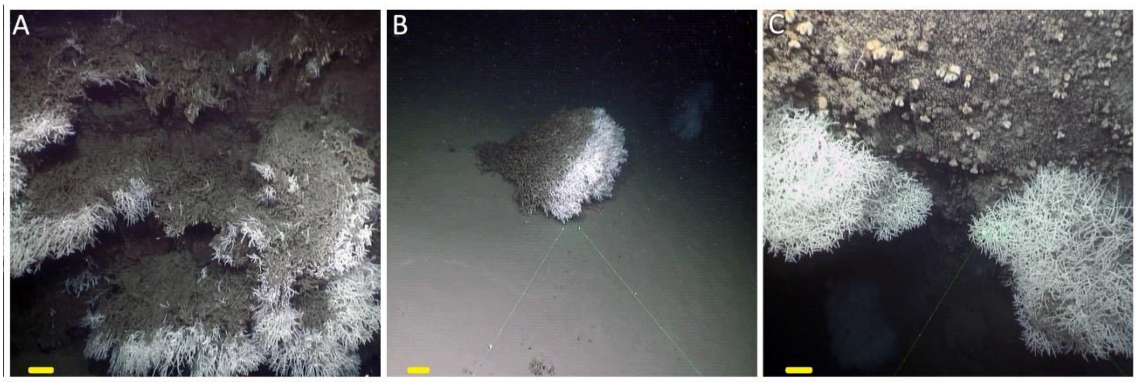


Figure 2.10. Colonial scleractinian growth patterns. *Madrepora oculata* on a canyon wall in the UCH (A); *Desmophyllum pertusum* on NE facing terrace in LCH (B); *Madrepora oculata* on a canyon wall in CHM (C). Scale bars: 10 cm (yellow).

Several species were found mostly among the LCH and CHM study sites, such as *J. cailleti*, *A. hirsuta, Placogorgia coronata*, *S. dubia*, *C. verticillata* and *A. dichotoma*, while in the OCH study site *A. dichotoma, J. cailleti* and *D. dianthus* were found (Fig 2.9). *L. glaberrima* was mainly found on the ECB (Fig. 2.8K).

Anitpahtes dichotoma, *J. cailleti*, *A. hirsuta* and *C. verticillata* were mostly observed around 1000 m depth, while *L. glaberrima* and *M. oculata* were found between 500 and 750 m depth. The other species showed a wider depth range, with mean values around 750 m depth (Fig. 2.11A). All coral species preferred high slope values (50–70°), especially black corals and the scleractinian *D. dianthus*, *J. cailleti* and *M. oculata* (Fig.

2.11B). Only *L. glaberrima* was mainly found on west facing slopes, while all the other coral species were mainly distributed on east facing slopes, especially *J. calietii*, *A. hirsuta*, *C. verticillata* and *A. dichotoma* (Fig. 2.11C).

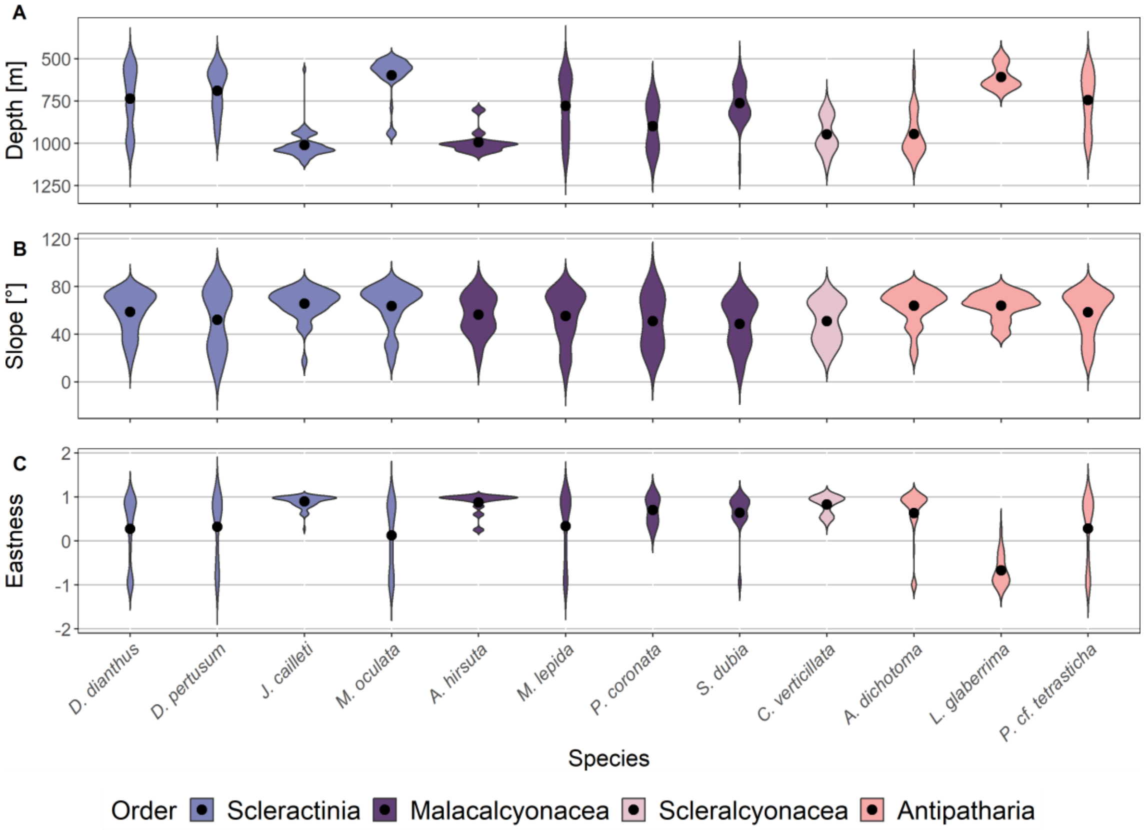


Figure 2.11. Coral distribution over gradients in the Blanes Canyon: depth (A), slope (B), and eastness (C).

2.3.5. Anthropogenic impacts

Total of 224 litter items were observed in the Blanes Canyon, and 35 trawl marks were observed in the canyon axis of LCH (Fig. 2.12A). Fishing lines were encountered 92 times, (157 lines), followed by fishing nets which were encountered 12 times, (18 nets) (Fig. 2.12B, C, D). Other plastic litter included: bags, bottles, sheets and other plastic objects. Metal, glass and textile litter items were encountered in forms of carpets, beverage cans and clothing (Fig. 2.12E, F, G, H, I, Table 2.5). The most common animals encountered growing to fishing lines were *M. oculata* (Fig. 2.12D) followed by *L. phalangium* and *D. dianthus*, while entanglement was recorded for *M. oculata* (Fig. 2.12C), *D. pertusum* and *C. cidaris* (Table 2.5). Spatial distribution of litter in Blanes Canyon shows that most items were found in the UCH and MCH, especially fishing nets and lines (Figure 2.13).

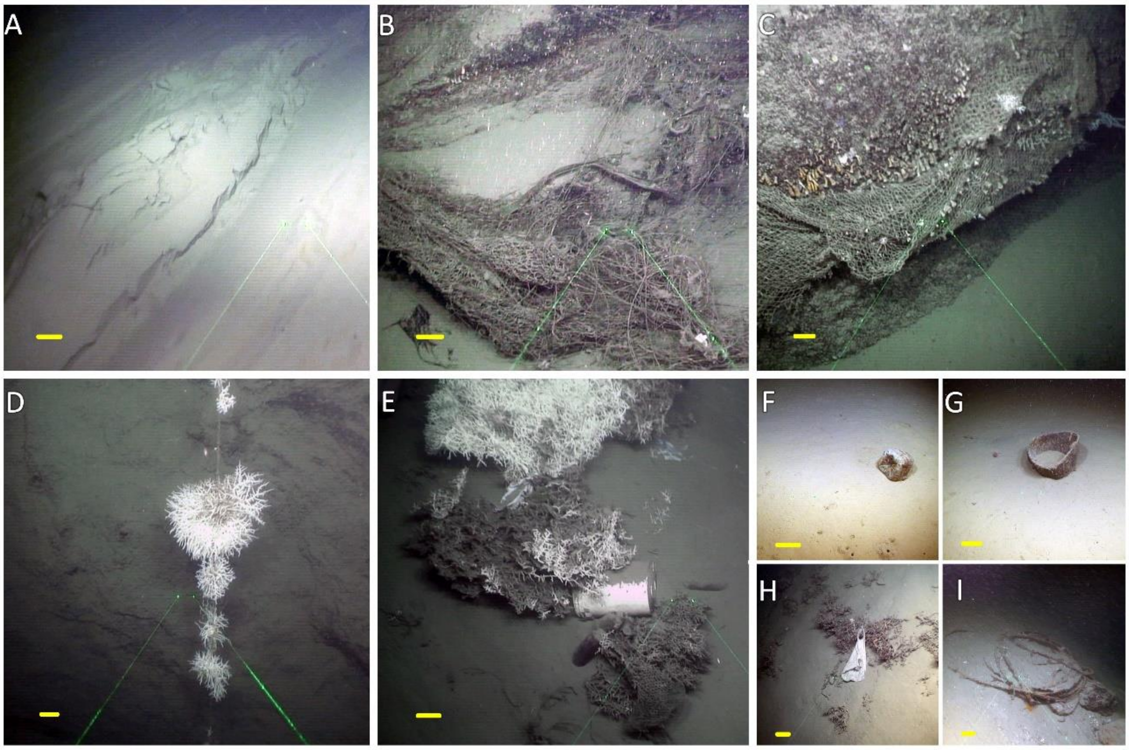


Figure 2.12. Anthropogenic impacts found in Blanes Canyon during the current study: Trawl marks (A), fishing net and fishing lines (B), fishing net (C), fishing line with *Madrepora oculata* (D), mixed items among coral rubble (E), plastic bottle (F), bucket (G), plastic bag (H), and metal cables (I). Scale bars: 10 cm (yellow).

Table 2.5. Litter categories found in Blanes canyon, showing density, depth and slope and type of interaction with species.

Litter category	Max density [item per m^2]	Mean ± SD density [item per m^2]	Mean ± SD Depth [m]	Mean ± SD Slope [°]	Type of interaction	Species
A1. Bags	0.4	0.3 ± 0.14	657.4 ± 49.3	15.9 ± 8.5		

A2. Bottles	0.4	0.24 ± 0.09	617.4 ± 56.2	27.3 ± 31.52		
A4. Sheets	0.4	0.21 ± 0.06	648.6 ± 100.8	38.31 ± 22.1		
A5. Other plastic objects	0.2	0.2	658.9 ± 98.8	15.4 ± 12.8		
A6. Fishing nets	1	0.3 ± 0.23	608.9 ± 44.7	32.4 ± 22.3	Attachment, Entanglement	*Leptometra phalangium, Cidaris cidaris, Desmophyllum pertusum, Madrepora oculata*
A7. Fishing lines	1.2	0.34 ± 0.24	583.2 ± 85.8	43.7 ± 18.5	Attachment	*Desmophyllum dianthus, Gracilechinus acutus, Leiopathes glaberrima, Desmophyllum pertusum, Madrepora oculata, Muriceides lepida, Sympagella delauzei, Tretodictyum reiswigi*
A8. Other fishing related	0.2	0.2	552.1	45		
A9. Ropes/strapping bands	0.2	0.2	569.2 ± 78.1	42.7 ± 17.2		
C1. Beverage cans	0.2	0.2	673.3 ± 37.8	10.7 ± 6.1		
C5. Cables	0.2	0.2	616.7	25.0		
C6. Fishing related	0.2	0.2	452.5	7.3		
D1. Bottles	0.2	0.2	552.1	45.0		
E1. Clothing (clothes, shoes)	0.2	0.2	670.7 ± 36.15	14.23 ± 6.6		

E2. Large pieces (carpets, etc.)	0.2	0.2	658.6 ± 59.9	34.4 ± 37.2		
I. Unspecified	0.2	0.2	727.6 ± 112.9	18.3 ± 19.03		

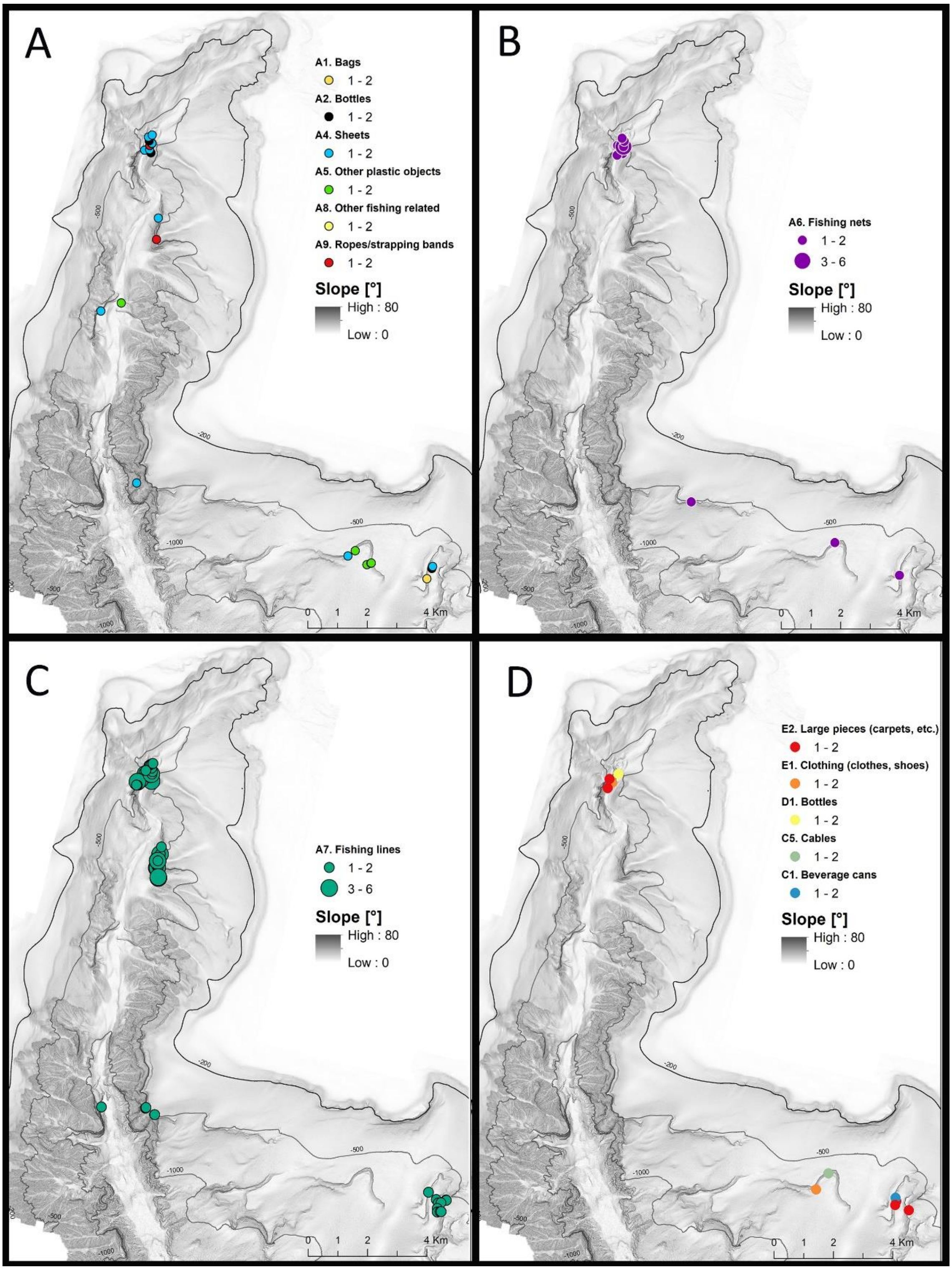


Figure 2.13. Litter category items in Blanes Canyon: Plastic (A), Fishing nets (B), Fishing lines (C), other items including metals, glass/ceramic and textiles.

2.4. Discussion

In Blanes Canyon five megabenthic assemblages were identified, two related to soft sediment and three found mosaiced on the canyon walls, without clear geographic separation.

Soft sediment assemblages were characterized by cerianthids (*Cerianthus* sp. and *Acananthus* sp.) and were found mainly on flat canyon axis or below the canyon walls, therefore deeper than the other assemblages. Previous observations from similar environments in Tyrrenian and Catalan canyons corroborate the findings in this study (Pierdomenico et al., 2019; Dominguez-Carrió et al., 2022).

The three canyon wall assemblages consisted mainly of sponges, corals and ascidians and did not show a specific geographic pattern. This reflects substrate heterogeneity as a dominant characteristic of canyon walls, that in Blanes Canyon encompasses patches of soft sediment among several types of hard substrate of middle-late Miocene age (ITGE, 1989). Some species in these assemblages tolerate more soft sediment deposition, such as several small round unidentified sponges, the annelid *B. viridis* and the carnivorous ascidian *D. antirrhinum*, which is considered a rare species in the Mediterranean, recently reported in La Fonera Canyon (5 ind.) and the Aeolian islands (29 ind.), while this study recorded 469 ind. (Mechó et al., 2014; Mastrototaro et al., 2019). In addition, some coral species are often reported in a mixed sediment environment such as *C. verticillata* and *S. dubia* (Fabri et al., 2014; Cau et al., 2015), composed of different substrates. However, most species were associated with steep slope sections of canyon walls with preference for biogenic-covered vertical walls, bare-rock vertical walls and rocky overhangs, along with mud-draped vertical wall which was the most common hard substrate type.

Between the prevailing corals, the rare bivalve *N. zibrowii* (max. 4 ind m^{-2}) was observed below overhangs, in presence of *D. dianthus* and *P.* cf. *tetrasticha* unlike in other studies, where it was associated with colonial scleractinians (Taviani et al., 2019, 2017). In addition, sponges *Tretodictyum reiswigi*, *P. compressa*, *P. monilifera*, *S. delauzei* and *Oopsacas minuta*, were found in close relation to CWCs, as reported in submarine canyons of the Catalan margin and Gulf of Lions (Boury-Esnault et al., 2017; Santín et al., 2018, 2019, 2021a). In this sense, previous studies on coral rubble collected from the same area had already highlighted the presence of a diverse poriferan assemblage (over 60 species confirmed) occurring within CWC assemblages in the Blanes Canyon (Santín et al., 2020b, 2021a, 2021b), which doubles the number of species/morphospecies identified in the present article. Nevertheless, given the inconspicuous nature of most of said species they cannot be reliably observed, less identified, by ROV alone, which is skewed towards bigger, exuberant species (Bo et al., 2012; Bertolino et al., 2019; Santín et al., 2021a), as is case for our present study. Notwithstanding the ROVs limited resolution for sponge identification, Porifera were still amongst the most diverse and abundant associated fauna within the observed CWC, highlighting the role of Mediterranean CWC as sponge diversity reservoirs (Bertolino et al., 2019; Santín et al., 2021a).

Canyon wall assemblages showed a preference for west canyon walls, a pattern that has been observed in the nearby canyons and linked with contrasting canyon morphology and hydro and sediment dynamics in the area (Orejas et al., 2009; Fabri et al., 2014; Lastras et al., 2016). In Blanes Canyon, the west canyon wall is steeper resulting in multiple long gullies and exposed overhangs that are environments very suitable for coral settlement and growth (Orejas et al., 2009; Huvenne et al., 2011; Lastras et al., 2011). The larger inclination suggests lower sedimentation rates compared to the more depositional east canyon wall and branch (Lastras et al., 2011; Durán et al., 2013). Moreover, the west wall is oriented against the prevailing geostrophic current direction (i.e.,the Northern Current), which is deflected by the Blanes Canyon and bringing nutritive particles from the coast and potentially larvae, and increasing the flow, reducing sediment deposition (Flexas et al., 2008; Lastras et al., 2011). Spatial heterogeneity of canyon walls is one of the crucial factors supporting submarine canyons as biodiversity hotspots (McClain and Barry, 2010; De Leo et al., 2014). This study mainly focused on the terrain-driven spatial heterogeneity that provided suitable habitat for megabenthic species and assemblages, however, the complex hydrodynamics of submarine canyons can further affect the spatial and temporal heterogeneity, contributing to the patchy distribution of benthic assemblages along the canyon walls (Ismail et al., 2018; Pearman et al., 2023).

The complex interaction between terrain variables and hydrodynamics has a defining impact on benthic assemblages, which has been found in submarine canyons around the world (Aguzzi, 2014; Brooke et al., 2017; Buhl-Mortensen and Buhl-Mortensen, 2005; van den Beld et al., 2017). In the canyons of Bay of Biscay, erosion of the northwestern flank due to dominate current exposes hard substrate that is populated by scleractinian corals (van den Beld et al., 2017). In some areas, sometimes in the absence of colonial scleractinians, other coral species are more dominant such as octocorals, however more studies should explore the underlaying reasons for this separation, including food requirements, aragonite horizon and tolerance on different environmental variables.

Supported by the species accumulation curves and rarefaction curves, high spatial coverage was achieved in most sites presented in this study. This permits an along-canyon distribution of CWCs to be discussed. In the UCH, colonial scleractinians (*D. pertusum* and *M. oculata*) were the main corals, alongside the bottle brush black coral *P.* cf. *tetrasticha*. Ecological indices showed relatively low biodiversity and evenness, which suggest an environment dominated by few species. *Desmophyllum pertusum* and *M. oculata* are frequently observed along the canyon heads on the Catalan margin and Gulf of Lions where *M. oculata* is several times more abundant than *D. pertusum*, although depth ranges reported in submarine canyons are generally shallower than in this study (Orejas et al., 2009; Gori et al., 2013; Fabri et al., 2014; Lastras et al., 2016; Lo Iacono et al., 2018; Dominguez-Carrió et al., 2022; Fabri et al., 2022). Submarine canyons and seamounts from the Atlantic show a strong impact of the Mediterranean Outflow Water (MOW) which flows at intermediate depths (500-1000 m depth). That water mass is considered important in CWC connectivity along the Bay of Biscay and towards the Azores, where many coral species (including ones mentioned in this work) are found (Dullo et al., 2008; Collart et al., 2018; Mosquera Giménez et al., 2019; Puerta et al., 2022; Taranto et al., 2023). There are several reasons why *M. oculata* is more abundant in the Mediterranean Sea, firstly it better adapts to higher temperatures, while *D. pertusum* better performs at colder areas such as found in the north Atlantic Ocean (Orejas et al., 2009; Roberts, 2009; Fossaa and Skjoldal, 2010; Gori et al., 2013). Interestingly, along the submarine canyons of Bay of Biscay, both species are equally important and abundant, distributed along the path of the MOW (Khripounoff et al., 2014; Arnaud-Haond et al., 2017; van den Beld et al., 2017). Study of Arnaud-Haond et al. (2017) mentioned that *M. oculata* occurs in small “bushes” in areas impacted by bottom-trawling, indicating its opportunistic strategy which could be a result from continuous reproduction and higher growth rates, compared to *D. pertusum* (Chemel et al., 2023). Colony sizes of these two species should be considered for future studies, heping to understand how these species co-exist.

Aymà et al. (2019) reports samples collected with an Agassiz trawl conducted along the Blanes Canyon axis between 752-1424m depth. From the data presented in this study it is not likely that CWCs are thriving in the canyon axis, which could imply the Agassiz trawl collected CWC that were already fallen from the canyon walls or were sampled close to the canyon wall (Aymà et al., 2019). However, this does not diminish the possibility of CWC living at larger depths, as is also shown in this study. *Paratipathes* cf. *tetrasticha* has not been frequently reported in the Mediterranean, and this study provides a detailed insight into its ecology. Unlike its congeneric species *P. larix*, *P.* cf. *tetrasticha* seems to occur at lower densities and larger depths (Bo et al., 2014). The fact that in this study *P.* cf. *tetrasticha* was found in the canyon head, steps out from the general perception of deep black corals as being vulnerable to e.g. high sediment loading (Fabri and Pedel, 2012; Wagner et al., 2012; Ocaña et al., 2017; Bo et al., 2020).

The canyon head is a hydrodynamic area that experiences high energy episodic events such as eastern winter storms or dense shelf water cascading that are characterized by high current velocities and high turbidity caused by coarse sediment displacement from the surrounding shelf (Sanchez-Vidal et al., 2012; Lopez-Fernandez et al., 2013a). These events can be detrimental or large, structurally complex animals such as *L. glaberrima* or *C. verticillata*. Small and simple shaped black corals grow in between colonial scleractinians that form extensive $CaCO_3$ frameworks which can thrive in these conditions. Furthermore, high sediment resuspension caused by frequent bottom trawling can affect the physiology of coral colonies, reducing growth patterns of these species and causing suffocation of upward facing polyps or premature detachment of the whole colony under growing weight of the sediment (Brooke et al., 2009; Larsson and Purser, 2011; Gori et al., 2013) (Chapter 4).

At the MCH and LCH, octocoral species abundance and species number increased, with species such as *C. verticillata*, *S. dubia*, and *M. lepida,* alongside the black coral *A. dichotoma*. Contrary to the UCH, these sites showed higher biodiversity and evenness, as well as an increase in mobile and rare species, which was probably due to increased soft sediment portions on these sites. Further along the canyon head, long, deep and vertical west canyon walls hosted almost all coral species of Blanes Canyon. These sites are still within the canyon head which has higher sedimentation rates than the open slope or further down the canyon (Paradis et al., 2018). Dating of sediment cores from the canyon head axis showed that since the 1970s, sedimentation rates increased which was attributed to the industrialization of the fishing fleet (Puig et al., 2015; Paradis et al., 2018). Moving further away from the fishing grounds, the sedimentation rates decrease to natural rates, i.e. rates that were measured in the canyon head before 1970s (Paradis et al., 2018). Additionally, studies regarding particle fluxes in Blanes Canyon showed that the particles are concentrated within the canyon head by closed circulation constrained by canyon topography (Palanques et al., 2005; Zúñiga et al., 2009; Lopez-Fernandez et al., 2013b). However, the impact of high energy episodic events is less intense which expands the environmental window where more species can thrive, e.g., based on our findings it is possible that the smaller polyp size and lower food requirements of octocoral and antipatharian species (Chapter 4) enables them to thrive in those depositional settings. Although more studies are needed to explain this pattern, the high diversity observed in this area highlights the high ecological importance of octocoral and antipatharian species.

Finally, the ECB was characterized by high densities of the octocoral *M. lepida* and antipatharian *L. glaberrima*. The number of species was similar to the UCH, but biodiversity and evenness were higher for the ECB. Conversely, colonial scleractinians were absent from this site. This part of the canyon is characterized by hemipelagic sedimentation processes governed by the along-margin advection of suspended particles by the Northern Current (Zúñiga et al., 2009; Durán et al., 2013), which can provide a more stable environment for the development of large and old colonies of *L. glaberrima* (Carreiro-Silva et al., 2013; Bo et al., 2015). Several other studies in the Mediterranean have observed *M. lepida* in high densities until 550 m depth, such as in Dohrn Canyon and the Corsica channel (Angeletti et al., 2020; Angiolillo et al., 2023) or on the Ligurian seamounts (Bo et al., 2021). The current study expands the range for this species to 1 118 m.

Desmophyllum dianthus was the only species that was found in all sites in Blanes Canyon, with high densities in the UCH and in the ECBe, emphasizing its role as a foundation species. In Blanes, *D. dianthus* grows downwards as in Chilean fjords (22–32 m depth) and La Fonera Canyon (600–1500 m depth) where it was suggested as an avoidance mechanism to high sediment concentrations (Försterra and Häussermann, 2003; Aymà et al., 2019). This species has been frequently recorded in the area, along the Catalan margin and Gulf of Lions, although no density values were reported (Orejas et al., 2009; Fabri et al., 2014; Gori et al., 2013; Lastras et al., 2016; Dominguez-Carrió et al., 2022). Its ubiquitous distribution in Blanes Canyon demonstrates its flexibility in terms of ecological and metabolic requirements, as it can adjust to a wide range of environmental conditions (Grange et al., 1981; Cairns, 1994; Försterra et al., 2017; Maier et al., 2021; Beck et al., 2022). Moreover, many octocorals and black corals were observed growing on live or dead skeleton of this species, showcasing its importance as a habitat former, a role that is often highlighted mostly for colonial scleractinian species (Grinyó et al., 2021).

The areas explored in this study ranged between 500 – 1200 m, which is a zone bathed by the Levantine Intermediate Water (LIW) and the West Mediterranean Deep Water (WMDW). The LIW flowing along the margin as a contour current from ~ 200 to 600 m depth, is proposed as a main driver of CWC distribution in the Mediterranean Sea, which poses Blanes Canyon both as a source and sink for CWC in the NW Mediterranean (Chimienti et al., 2019; Hayes et al., 2019). Assemblages and species found in Blanes Canyon are in accordance with other findings from the Mediterranean Sea below 200 m depth (Mastrototaro et al., 2010; Fabri et al., 2014; Taviani et al., 2017; Grinyó et al., 2018; Pierdomenico et al., 2019; Taviani et al., 2019; Dominguez-Carrió et al., 2022). However, most studies of submarine canyons from the Catalan margin and Gulf of Lions were restricted to a maximum of 550 m depth, making comparisons with the current study difficult. Further studies on the shallower regions of Blanes Canyon and deeper areas of other canyons are therefore required. This would also contribute to understanding the role of the WMDW in CWC and associated fauna distribution, which is likely crucial for deep dwelling species such as *J. cailleti* (Sartoretto & Zibrowius, 2018, Taviani et al., 2019; Angeletti et al., 2020).

Overall, this study showed that Blanes Canyon is a “typical Mediterranean” setting as the main colonial scleractinian was *M. oculata*, for which is considered to better handle current environmental conditions than *D. pertusum* which more frequently found in the Atlantic (Fabri et al., 2014; Maier et al., 2019a; Vertino et al., 2019). Alongside, another important Mediterranean aspect is the role of LIW as an intermediate water where most CWCs are found (Chimienti et al., 2019; Hayes et al., 2019). This ties nicely with findings in “typical deep sea” environment where the intermediate waters have an important role in connectivity of CWC patches, e.g., the Mediterranean Outflow Water (MOW) in the north Atlantic (Arnaud-Haond et al., 2017; Boavida et al., 2019b; Mosquera Giménez et al., 2019; Puerta et al., 2022; Taranto et al., 2023). Finally, one of the most “typical canyon” settings are the steep canyon walls that provide habitat for CWCs and other species, enriching canyon productivity (Huvenne et al., 2011; Fernandez-Arcaya et al., 2017; Pearman et al., 2023).

Anthropogenic impacts, despite the ones caused by bottom trawling resuspension, were also recorded in Blanes Canyon, mainly as lost fishing gear such as fishing lines and nets entangled on rocky outcrops on the canyon walls, similar to other reports from the Gulf of Lions and Catalan margin (Fabri et al., 2014; Lastras et al., 2016; Dominguez-Carrió et al., 2020; Santín et al., 2020a). Spatial distribution of lost fishing gear is concentrated in the canyon head, which is aligned with other studies that highlight the importance of canyon topography and hydrodynamics in litter dispersal (Cau et al., 2017; Pierdomenico et al., 2019; Dominguez-Carrió et al., 2020; Hernandez et al., 2022). In case of older fishing lines, corals and sponges were found attached and growing on them. These corals will not be able to reach large sizes as the fishing line will collapse with their growing weight and they could be dislodged to a less suitable area for further growth. Also, associated fauna of these floating colonies is probably different to the ones found on stable substrate.

Along with lost fishing gears, the main anthropogenic impact in Blanes Canyon is related to bottom trawling targeting the blue and red shrimp *Aristeus antennatus,* that takes place on the canyon flanks and rims. High sedimentation rates (0.2-2.1 cm yr^{-1}) reported in the Blanes Canyon axis are related to downslope transport of resuspended sediment caused by bottom trawling in the area (Paradis et al., 2018). Similar sedimentation values are found in nearby La Fonera Canyon (2.4 cm yr^{-1}), where as in the case of Blanes Canyon, the increase in sedimentation rate was found after 1970s due to industrialization of the fishing fleet (Puig et al., 2015; Paradis et al., 2018). This type of sediment transport was recorded on a daily basis in nearby canyons in the form of turbidity currents of high suspended sediment concentrations (Martín et al., 2014a, 2014b, 2014c; Puig et al., 2014; Arjona-Camas et al., 2019, 2021). Moreover, the suspended sediment can interfere with polyp activities such as respiration and feeding, causing polyp mortality in extreme events (Larsson et al., 2013b; Lartaud et al., 2017; Bollati et al., 2022; Tuttle and Donahue, 2022)(Chapter 4). Initial protection provided by canyon steep topography to species living on canyon walls is compromised when surrounded by fishing grounds (Huvenne et al., 2011; Puig and Gili, 2019).

In this study we recorded densities of several endangered species of CWC such as *L. glaberrima*, *D. pertusum*, *D. dianthus* and *M. oculata* as defined by the IUCN Red List (Otero et al., 2017). Even though the General Fisheries Commission for the Mediterranean (GFCM) encourages a restricted fisheries area (FRA) below 1 000 m depth in the Mediterranean, this exceeds the optimal depth range for CWCs in the Mediterranean that is usually considered between 300 – 700 m depth where LIW is dominant (FAO, 2020). Despite Blanes Canyon is not within any current marine protected area or conservation action, this study provides sound bases for future considerations within the frame of effective spatial management and environmental planning (Huvenne and Davies, 2014; Fernandez-Arcaya et al., 2017).

3. CHAPTER 3: Water column characterization in areas close to cold-water corals of Blanes Canyon and an insight into effects of bottom trawling sediment resuspension

3.1. Introduction

Understanding the environmental conditions (and their variability) in areas of high biodiversity importance, such as submarine canyons, is important. The role of water masses is increasingly recognized as important for the distribution of cold-water corals (CWCs) (Mosquera Giménez et al., 2019; Puerta et al., 2020, 2022; Taranto et al., 2023). Temperature and salinity are the main descriptors of water masses, and they are known to be important factors for CWC distribution and physiological performance (Naumann et al., 2013; Gori et al., 2014a, 2016; Puerta et al., 2020). As suspension feeders, CWCs are found in hydrodynamic areas with varying current velocities that supply them with food (Duineveld et al., 2004; Purser et al., 2010; Mienis et al., 2012).

The interplay between canyon topography and local hydrodynamics causes a palette of distinct oceanographic conditions that play important roles in different life stages of marine species (Puig et al., 2001; De Leo et al., 2010; Pearman et al., 2023). For example, within canyons, areas of the water column with higher suspended sediment concentrations (SSC), known as nepheloid layers are commonly found near the bottom and at intermediate depths (Puig and Palanques, 1998; Wilson et al., 2015b). Nepheloid layers harbour increased particulate organic matter (POM), live zooplankton and larvae, which can be important sources of nutrition for suspension feeders like CWCs (Puig et al., 2001; Mienis et al., 2007; Huvenne et al., 2011; Fernandez-Arcaya et al., 2013).

Blanes Canyon has been identified as an important CWC habitat, harbouring 12 CWC species and their associated fauna (Chapter 2). The major anthropogenic impact surrounding Blanes canyon is bottom trawling that takes place on the continental shelf and slope surrounding the canyon, as well as on its flanks, rims and partly in the canyon axis (Sardà et al., 2009; Paradis et al., 2018; Soriano et al., 2020) (Fig. 1.2.). Indirect impacts of bottom trawling on submarine canyons have been studied along the Catalan margin (Palanques et al., 2006b; Puig et al., 2012; Martín et al., 2014a, 2014c; Arjona-Camas et al., 2019, 2021; Paradis et al., 2020) and in Blanes Canyon (Paradis et al., 2018). Trawling causes resuspension of large quantities of sediment which are transferred into the canyon by currents, leading to high SSC and sediment accumulation in the axis (Paradis et al., 2018). In addition, alongside sediment, trawling suspends large quantities of other particles, including organic matter of poor nutritional quality (Lopez-Fernandez et al., 2013b; Pusceddu et al., 2014a; Wilson et al., 2015a; Daly et al., 2018).

Increased sedimentation and SSC can harm CWCs, as it may cause tissue injury, clogging of feeding structures and physiological stress (Brooke et al., 2009; Larsson and Purser, 2011; Larsson et al., 2013a; Liefmann et al., 2018) (Chapter 4). Moreover, resuspension of sediment and organic particles collectively alter the water column properties, with possible negative impacts for the survival and prevalence of CWC species. Despite the importance of CWCs as habitat forming species in Blanes Canyon, and the vicinity of the canyon to trawling grounds, up to date there is limited knowledge on how trawling may alter CWC habitat (Juan et al., 2007; Pusceddu et al., 2014b; Pierdomenico et al., 2018; Rijnsdorp et al., 2018). This Chapter describes the oceanographic conditions and the compositional analyses of suspended particles in areas within Blanes Canyon next to CWCs presence and evaluates changes on these conditions provoked by trawling sediment resuspension along the canyon axis.

3.2. Materials and methods

3.2.1. Water column characterization

3.2.2.1 Along canyon casts

The flanks of the Blanes Canyon were explored with ROV during the ABRIC 1 cruise on board the R/V *Sarmiento de Gamboa* in February 2020 (Chapter 2). After each ROV dive, three CTD casts were performed in the vicinity of the explored area (Fig. 3.1A) with a SeaBird SBE 911 plus with a turbidity sensor and coupled to a SBE 32 Carousel Water Sampler Frame with 12 L bottles. At the last CTD cast water samples were taken at 5, 50, 100 and 200 m above the bottom (mab) as well as at the chlorophyll maximum depth with the aim of quantifying suspended particulate matter (SPM), particulate organic nitrogen (PON), particulate organic carbon (POC), total lipids (TL) (except for the chlorophyll maximum depth) and chlorophyll a (Chl-a) (only for the chlorophyll maximum depth). At each sampling depth, 50 ml water sample was also taken for the quantification of nutrient concentrations (ammonium, nitrites, nitrates, phosphate, and silicate) which was stored at -20°C until analysis. Description of handling other water samples is described in section 3.2.2.3.

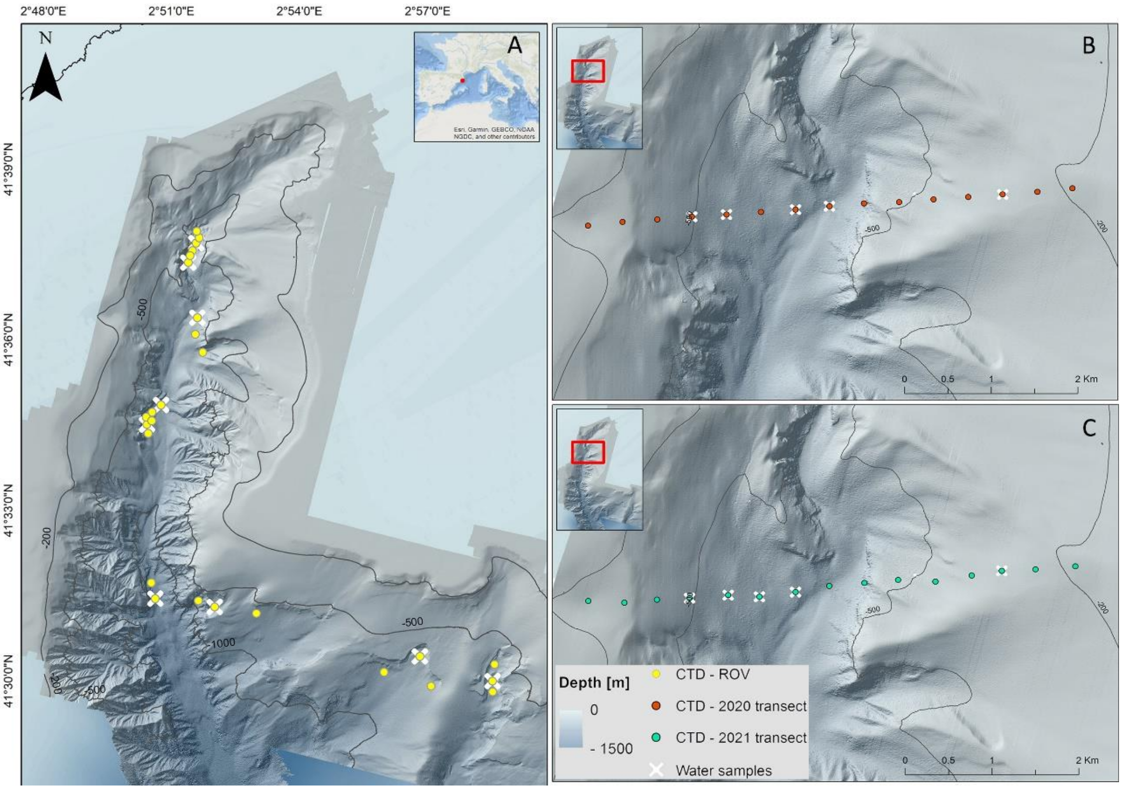


Figure 3.1. Blanes Canyon. CTD casts along the canyon, located close to CWC locations reported in Chapter 2 (A); CTD casts located across the canyon transect performed in 2020 (B); and 2021 (C). White crosses indicate locations of water sampling.

3.2.2.2 Across canyon transects

A transect of CTD casts was preformed across the canyon head and the adjacent fishing grounds (Fig. 1.2) on the shelf in two consecutive years, with the aim of characterizing bottom nepheloid layers (BNL) induced by bottom trawling fishing activity (Fig. 3.1B, C). The characterization focused on SPM, total carbon (TC), POC and total nitrogen (TN). The initial plan of repeating the transect in the same year (comparing fishing closure and fishing season time) was interrupted by COVID-19 lockdown, so the transect was repeated after 11 months instead. In February 2020 (fishing closure) the transect was performed during the ABRIC-1 cruise on board the R/V *Sarmiento de Gamboa* and consisted of 15 CTD casts along 5.6 km distance, with water sampling performed at 5 mab at several stations located on the fishing grounds and the canyon axis (Fig. 3.1B). In

January 2021 (fishing season), the transect was repeated during the ABRIC 2 cruise on board the R/V *SOCIB* by performing 15 CTD casts within average 35 m accuracy (Fig. 3.1C). Since it was fishing season, trawling vessels were operating in the area, thus water sampling 5 mab was performed at the same stations as during ABRIC-1, except for station 6 that was opportunistically sampled during ABRIC-2 cruise following the passage of a trawling fishing vessel, instead of station 8 as sampled in ABRIC-1. This gave the opportunity to observe the BNL immediately after the passage of a bottom trawling vessel. All casts and water sampling were performed with a SeaBird SBE 911 plus coupled to a SBE 32 Carousel Water Sampler Frame with 12 L bottles.

3.2.2.3 Water filtering and analysis

Collected water was filtered on board onto 47 mm GF/F filters after which the filters were immediately frozen at -20°C until analysis. Volumes filtered varied based on designated analysis, so for Chl-a 5 L were filtered, for TL 7.8 ± 0.45 L and for SPM and subsequent elemental analysis 8.0 ± 0.85 L were filtered. These volumes were chosen to maximize the effort and get enough material for analysis, as we did not have a stand alone pump (SAPs) like in similar studies (Kiriakoulakis et al., 2011). The volumes differed (hence the standard deviation) in cases when CTD bottles would not close. SPM was quantified for all samples by subtracting the initial weight of the filter acquired before filtration, from the weight found after drying the filters at 36°C for 48h. Afterwards, filters from CTD casts along the canyon (close to CWC locations) were separated from the filters from the CTD casts across the transect in both years. This was done because we were interested in the TC and POC from the across canyon transects due to potential impact of fishing activities, while only POC was considered for the samples close to CWC locations. In order to obtain these values for the across canyon transect samples, we cut the filters in half, where one half was maintained unchanged and the other underwent acidification along with the filters from along the canyon (close to CWC locations). This was done according to Yamamuro and Kayanne (1995) and Kiriakoulakis et al. (2011) (Yamamuro and Kayanne, 1995; Kiriakoulakis et al., 2011). The filters were stored during 24h at room temperature in a tight-shut chamber containing a 10 ml beaker with 12N HCl, which produced an acid-fumed atmosphere to remove carbonates. After removing the filters from the acid atmosphere, they were kept in a fume hood during 6h and transferred to 36°C where they were kept for 48h before being shipped for elemental analysis. Carbon and nitrogen concentration was quantified with a FlashEA1112 elemental analyser (ThermoFinnigan), equipped with a MAS200R autosampler, based on ¼ of a filter.

TL was quantified by leaving the filters in 6 ml of chloroform–methanol (2:1) overnight followed by spectrophotometric quantification using cholesterol as a standard (Barnes and Blackstock, 1973). Chl-a content was measured with a sensitive fluorometer following extraction with 85% acetone (Yentsch and Menzel, 1963). Water samples kept for nutrients at -20°C were thawed just before analysis and analysed with Continuous-Flow Analysis AutoAnalyzer 3 (Seal Analytical).

3.2.2.4 CTD cast analysis

CTD casts were processed with SBE Data Processing software, while the visualisation of the data was performed in Ocean Data View (Schlitzer, 2015). Turbidity measurements, recorded in FTU (Formazine turbidity units) were converted to excess suspended sediment concentration (xs-SSC, in mg/L) following (Puig et al., 2013) and using the slope of the regression line derived experimentally using canyon axis sediments from the neighbouring Palamós Canyon (xs-SSC _= 1.14 FTU ($r^2 = 0.99$)) (Arjona-Camas et al., 2021).

3.2.2. Fishing activity

Fishing activity was accessed only for the dates when across canyon CTD transects were performed, 24/02/2020 (during ABRIC-1) and 20/01/2021 (during ABRIC-2) using data from the Automatic Identification System (AIS) downloaded from Shiplocus (Puertos del estado). As mentioned above, ABRIC-1 cruise was done during fishing closure and no fishing activity was found.

Data collected for 20/01/2021 showed fishing activity which was processed based on speed over ground (Sog) in R (R Core Team, 2022). Bimodal distribution was found for Sog values, where the first Gaussian distribution is related to trawling activities, while the second is related to navigation (Oberle et al., 2016; Shepperson et al., 2018) (Fig. 3.2). In order to isolate the fishing activities based on the first Gaussian distribution, only Sog between 0.1 and 5 knots (kn) were considered. Furthermore, mean ± 2 standard deviations were calculated in order to obtain trawling speeds (0.235 and 3.579) (Fig. 3.2). Due to relatively small dataset, manual confirmation was performed to check for false-positive or false-negative values. Data visualization was performed in *ggplot2* (Wickham H, 2016) and ArcGIS 10.4.

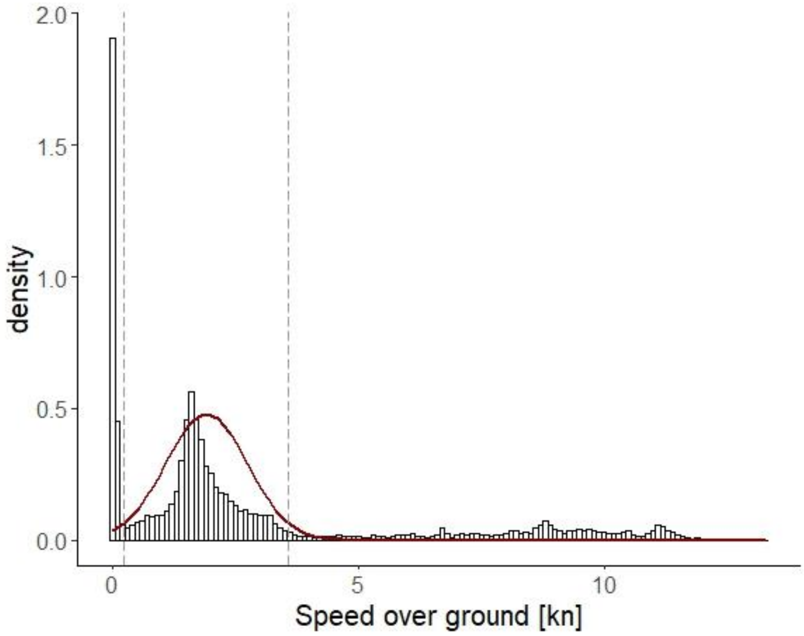


Figure 3.2. Distribution of vessels speed over ground (Sog) for 20/01/2021 over Blanes Canyon. Vertical dashed lines are limits of what is considered fishing activity in this study (0.235 and 3.579 kn)

3.2.3. Statistical analysis

Principal Coordinate Analysis (PCoA) was performed using a dissimilarity matrix based on Euclidian distances using *cmdscale* function from vegan package in R (Oksanen et al., 2022). The analysis was performed on POC, PON and C/N ratio data from water samples collected close to the CWC locations, excluding the chlorophyl maximum sampling station, since the objective was identifying if there was clustering of BNLs.

3.3.Results

3.3.1. Water masses

Water masses found in Blanes Canyon include modified Atlantic Water (mAW), Western Intermediate Water (WIW), Levantine Intermediate Water (LIW) and West Mediterranean Deep Water (WMDW) (Fig. 3.3). Relative dominance of surface water masses (mAW and

WIW) differed between the two years, where mAW was mostly found in 2020, while was absent in 2021 (Fig. 3.3). WIW was present in both years, although in 2020 it was warmer and deeper, found between mAW and LIW, notable as a “V” shape between the two water masses (Fig. 3.3a), compared to 2021 where WIW was the prevailing water mass in the surface with relatively low temperatures (Fig. 3.3b). Below the surface waters, LIW core is found between 400-600 m depth, and deeper is the WMDW (Fig. 3.3). LIW is known as a warm and saline intermediate water mass, notable as a hump in a TS diagram. The WMDW is found deeper, characterized as a colder and saline water mass. Based on data in this study, the latter two water masses remained stable between the two years.

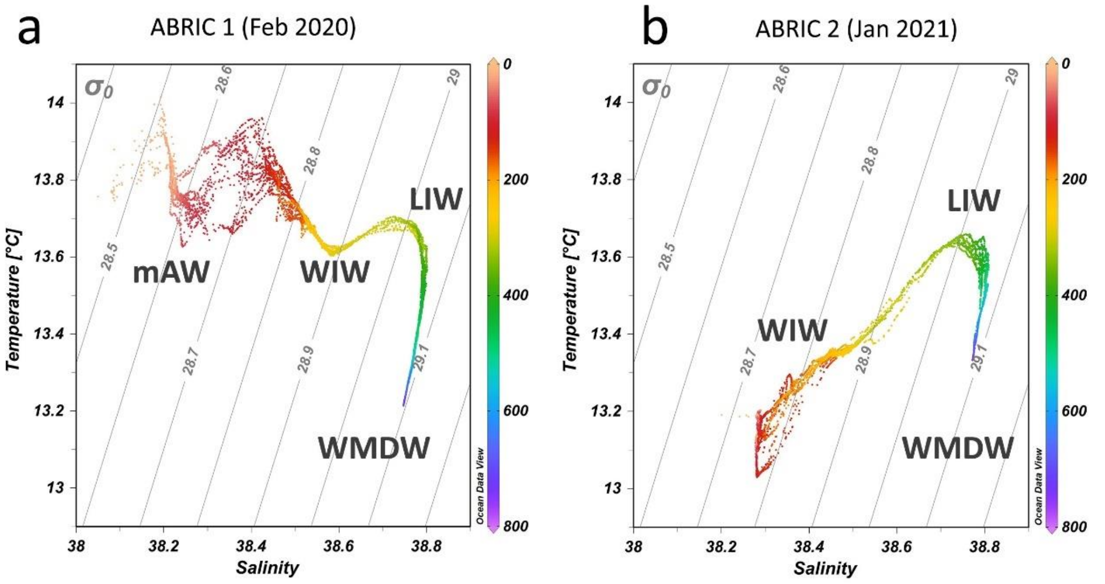


Figure 3.3. TS diagrams based on CTD casts conducted across the canyon transect in ABRIC 1 (February 2020) (a) and ABRIC 2 (January 2021) (b). Water masses abbreviated as follows: modified Atlantic Water (mAW), Winter Intermediate Water (WIW), Levantine Intermediate Water (LIW), Western Mediterranean Deep Water (WMDW).

3.3.2. Across canyon transect and impact of bottom trawling

Water masses characteristics found across the canyon transect between two years are presented in Figure 3.4. Temperature of surface waters in 2020 was >13.8°C (Fig. 3.4a), while in 2021 it was 13.2 – 13.4°C (Fig. 3.4b), which is due to different water masses described above. Salinity was less variable between the two years, reaching values < 38.4 (Fig. 3.4.c, d). Below 400 m depth, both temperature and salinity were more stable (T~13.6-13.8°C; S~38.6) (Fig. 3.4.).

In case of xs-SSC, in 2020 the xs-SSC values showed only the presence of a thin bottom nepheloid layer in the canyon axis (~ 0.2 mg/L, Fig. 3.3e). High xs-SSC in 2021 was concentrated to the location following a trawling activity, while the bottom nepheloid layer in the canyon axis had a larger extension, compared to previous year (Fig. 3.3f).

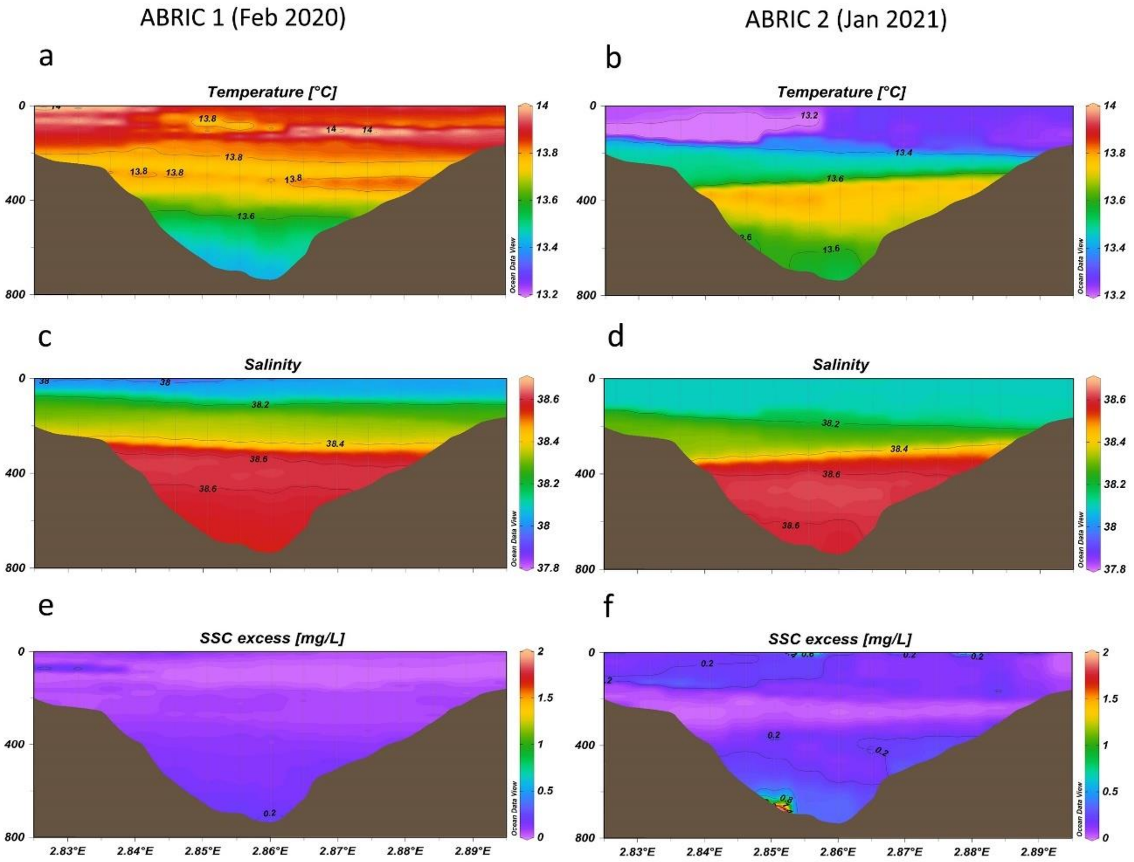


Figure 3.4. Water column characteristics based on across canyon transect during ABRIC 1 (February 2020) (a, c, e) and ABRIC 2 (January 2021) (b, d, f); temperature (a, b); salinity (c, d); excess of suspended sediment concentration (SSC) (e, f).

Bottom trawling resuspension in Blanes canyon was registered only in January 2021, when the fishing season was open. On the day of sampling (20/01/2021), the fishing activities were concentrated to a fishing ground partially passing through the canyon axis, based on AIS data, where in total four fishing vessels were recorded completing 10 hauls (Fig. 3.5a). Station 6 (ST06) was located on that fishing ground where turbidity expressed as xs-SSC reached maximum of 6 mg/L near the bottom (680 m depth), which decreased to 0.5 mg/L at 660 m depth and was maintained as such until 560 m depth (Fig. 3.5d, e). Comparatively, during fishing closure the xs-SSC values were steady throughout the water column, mostly below 0.2 mg/L (Fig. 5b, c).

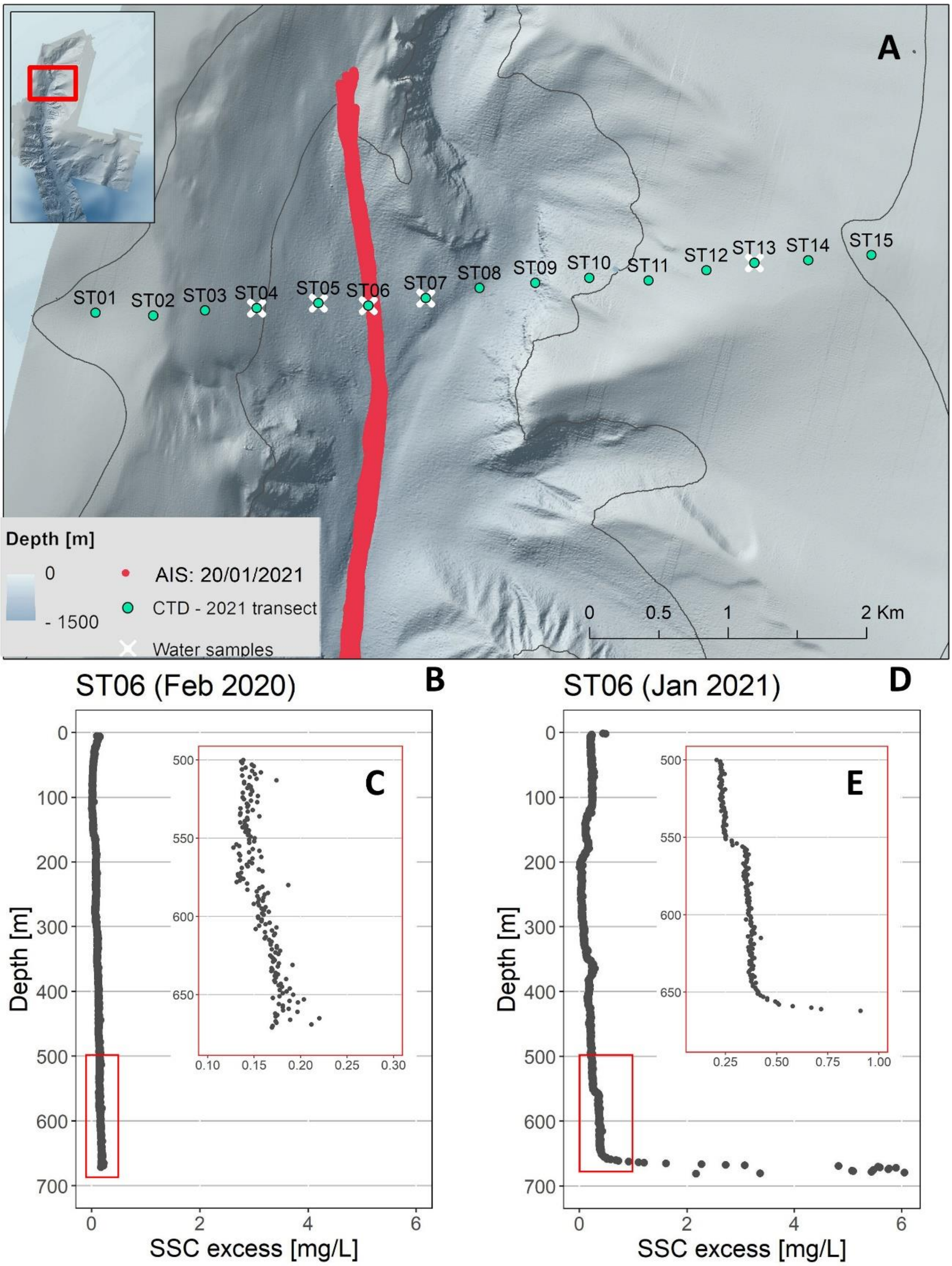


Figure 3.5. Bottom trawling fishing activity in Blanes canyon on 20/01/2021 (A); depth profile of excess of suspended sediment concentration (SSC) at station 06 (ST06) during ABRIC 1 (B); detail of (B) (C); depth profile of excess of suspended sediment concentration (SSC) at station 06 (ST06) during ABRIC 2 (D); detail of (D) (E).

Elemental analysis of bottom nepheloid layers (BNL) sampled during two ABRIC cruises is shown in Figure 3.6. Excess of SSC was the highest at ST06 during ABRIC-2 (5.7 mg/L), alongside adjacent stations (S05 and S07) that had lower values (~0.4 mg/L) (Fig. 3.6A). SPM was the highest at ST06 where the mean value was 2.39 ± 0.08 mg/L (Fig. 3.6B). TC, POC and TN were higher during ABRIC 2 at all sampling stations compared to ABRIC-1, where the highest values were found at ST05 and ST06 (Fig. 3.6C, D, E). More specifically, TC values averaged among all stations sampled during ABRIC-2 reached a mean value of 104.76 ± 37.73 µg/L, POC values reached a mean value of 79.32 ± 20.67 µg/L and TN values reached mean value of 6.53 ± 2.21 µg/L (Fig. 3.6C, D, E). Comparatively, during ABRIC-1, TC mean value was 46.52 ± 10.37 µg/L, POC reached a mean value of 39.77± 15.61 µg/L while TN had a mean of 2.54 ± 0.66 µg/L (Fig. 3.6C, D, E).

However, molar C/N ratio was high in both cruises, reaching mean values of 19.7 ± 12 during ABRIC 1 and 14.8 ± 3.17 during ABRIC-2 (Fig. 3.6F).

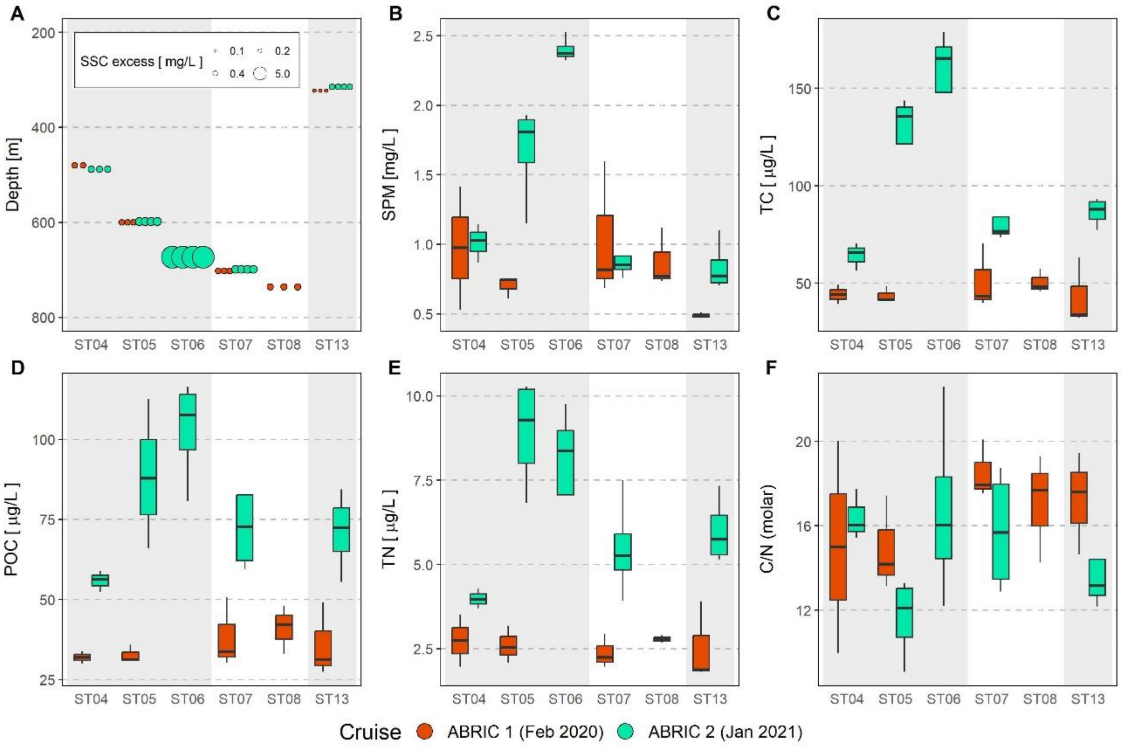


Figure 3.6. Comparison between bottom nepheloid layers (5 mab) sampled during two cruises (ABRIC-1 and ABRIC-2) showing suspended sediment concentration (SSC) (A); suspended particulate matter (SPM) (B); total carbon (TC) (C); particulate organic carbon (POC) (D); total nitrogen (TN) (E); and molar C/N ratio (F).

3.3.3. Along canyon casts

The water masses found along the canyon in ABRIC-1 were the same as found in the transect that year (see above), with addition of WMDW, found below 800 m ($T < 13.1$ °C, $S = 38.7$, $\rho > 29.1$) (Fig. 3.7C2, D2). Depth profiles of xs-SSC showed a pronounced BNL in the upper canyon head (UCH) and mid-canyon head (MCH) between 400-700 m depth, reaching 0.2 mg/L (Fig. 3.7A3,4 and B3). Deeper stations such as in the lower canyon head (LCH) showed an increase between 400-700m as well, which was maintained until the bottom (Fig. 3.7C3,4). The canyon head mouth (CHM) hosted the deepest station reaching 1200 m depth where the SSC profile fluctuated around 0.1 mg/L, showing an increase between 400-600 m depth and 800-1000m depth (Fig. 3.7D3). BNL at the stations of the east canyon branch (ECB) was lower compared to the UCH, reaching

0.1 mg/L (Fig. 3.7E3,4). Based on the data provided in Chapter 2 of the thesis CWC presence coincides with the BNL and the water samples taken.

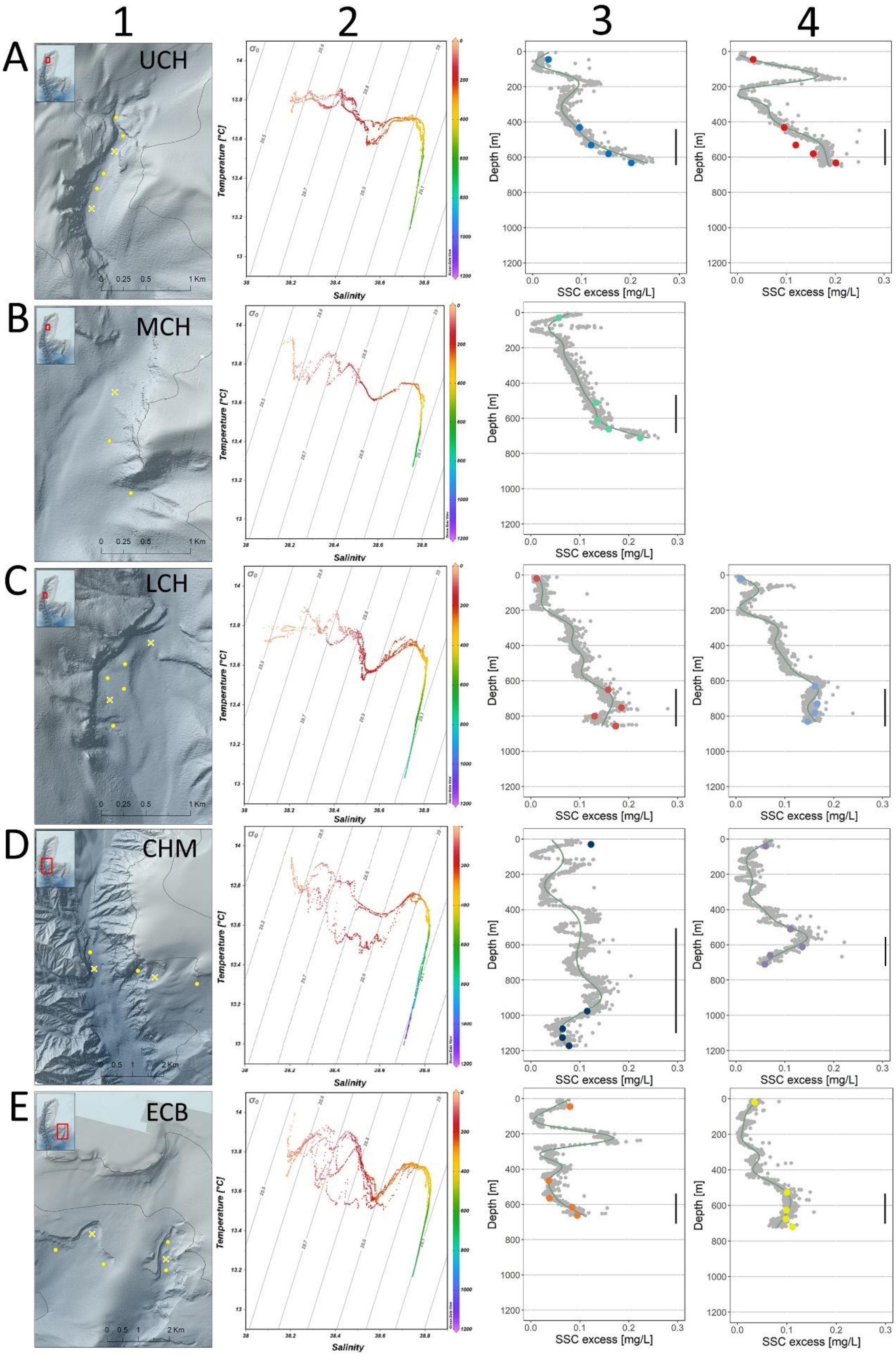


Figure 3.7. Locations of the water samples (1), TS diagrams of the CTD casts (2), turbidity profiles for each of the stations where water sampling took place (3,4), indicated with larger coloured points. The black bars in each graph mark the presence of CWC based on Chapter 2.

Upper canyon head (UCH) (A); mi canyon head (MCH) (B); lower canyon head (LCH) (C); canyon head mouth (CHM) (D); east canyon branch (ECB) (E).

Nutrient analysis showed expected values for West Mediterranean Sea (Fig. 3.8). The chlorophyll maximum was found between 20-50 m depth with mean value 0.27 ± 0.09 mg/L. Phosphate, nitrate and silicate measured at this sampling depth showed minimum values of 0.03 ± 0.01 µmol/L, 1.33 ± 0.84 µmol/L, 1.36 ± 0.28 µmol/L, respectively (Fig. 3.8). Nitrite was found at its maximum reaching values 0.28 ± 0.06 µmol/L, while ammonium was relatively constant with depth, reaching mean value of 0.1 ± 0.04 µmol/L at chlorophyll maximum (Fig. 3.8).

Sampling stations below the chlorophyll maximum depth ranged between 431 – 1173 m. Within this depth range phosphate and nitrite showed little variability with depth, 0.38 ± 0.02 µmol/L and 0.01 ± 0.004 µmol/L, respectively (Fig. 3.8). Nitrate followed a general increase with depth (8.03 ± 0.98 µmol/L), however slightly lower values are noticeable around 600 m (Fig. 3.8). Silicate showed increase with depth with mean value at 5.76 ± 0.57 µmolL-1 (Fig. 3.8).

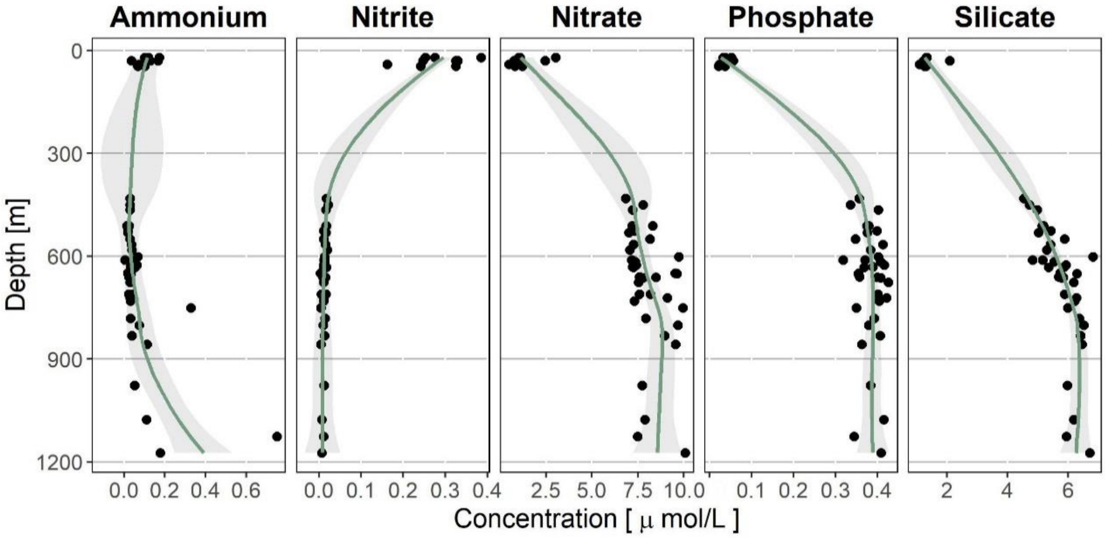


Figure 3.8. Dissolved inorganic nutrient depth profiles along Blanes canyon. Please refer to Figure 3.7 for location of water sample casts.

SPM did not have a pronounced depth profile with average value 0.65 ± 0.15 mg/L, however a slight decrease was found below 900 m depth (Fig. 3.9). POC and PON had higher values in the chlorophyl max (ChlMax) sampling depth with mean value at 69.85 ± 33.22 µg/L and 14.17 ± 4.74 µg/L, respectively (Fig. 3.9). The mean values recorded in the deeper sampling depths for POC were 25.76 ± 12.8 µg/L while for PON were 5.72 ± 2.57 µg/L (Fig. 3.9). Molar C/N ratio was 5.68 ± 1.27 at the ChlMax sampling depth, but an increase was visible at larger depths with a mean value of 6.29 ± 3.35. TL were only measured for deeper sampling stations, showing high variability and average value at 15.48 ± 7.99 µg/L (Fig. 3.9).

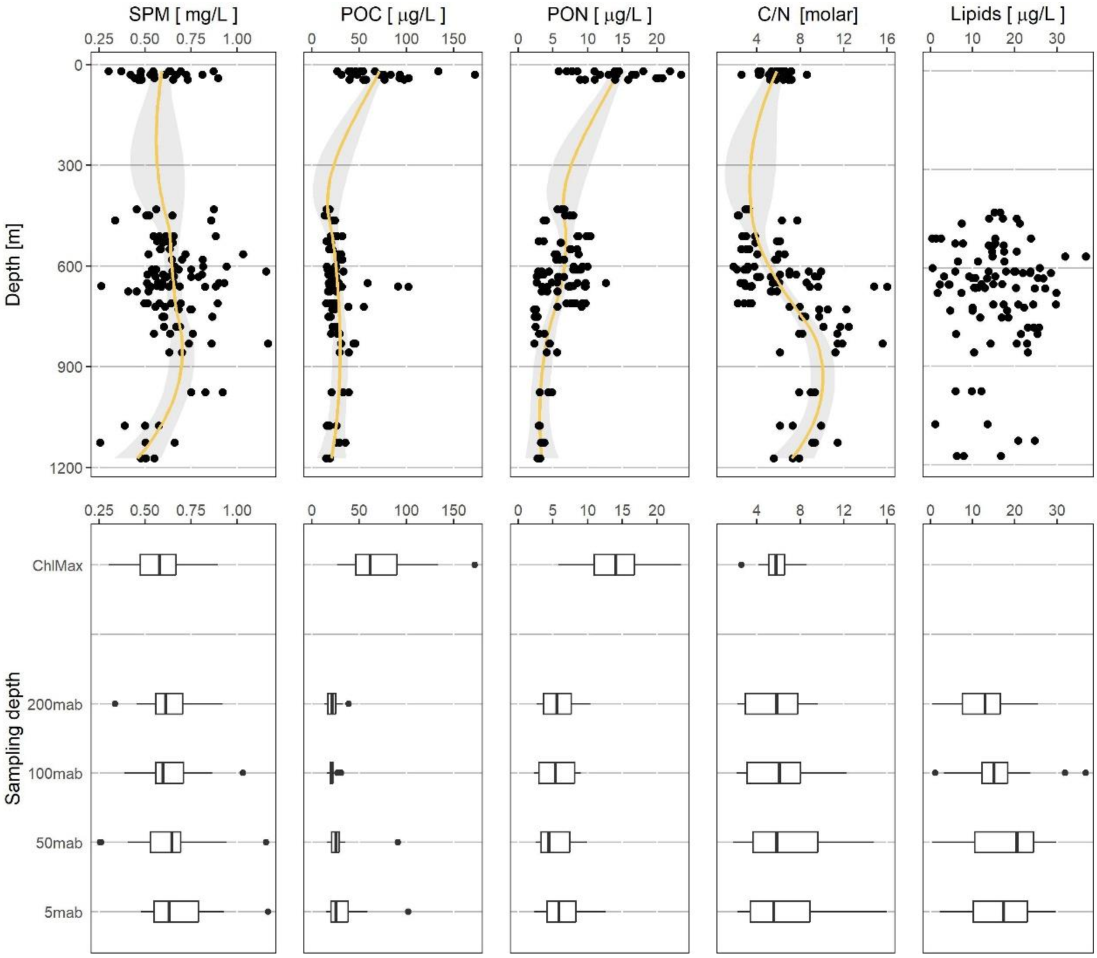


Figure 3.9. Suspended particulate matter (SPM), particulate organic matter (POC), particulate organic nitrogen (PON), molar C/N ratio and total lipids depth profiles along the canyon at five sampling depths. The first row shows data continuously along depth and the second row shows the same data separated by sampling depths. Abbreviation: meters above bottom (mab). Please refer to Figure 3.7 for location of water sample casts.

Differences between stations in POC, PON and molar C/N ratio were found when concentrating on deeper sampling depths (Fig. 3.10). POC was relatively similar between stations, where a slight increase was found at ~ 600 m depth and ~ 800 m depth. PON values were higher at the stations closer to the coast, therefore also shallower. Exception was CHM04 which is further from the coast but within the same depth range as the stations closer to the coast (Fig. 3.10B, D). On the other hand, stations on the ECB which are furthest from the coast, while in the same depth range as the first group, showed lower PON values (Fig. 3.10B, D). Deeper stations belonging to the LCH group and CHM02 showed lower PON values as well. Additionally, the changes in PON impacted the molar C/N ratio where stations closer to the coast had lower values compared to the rest (Fig. 3.10C). Principal coordinates analysis recognized this discrepancy as well grouping together stations closer to the coast against stations further from the coast and deeper, where the first axis explains 22.4 % of the variation and the second 14.4% (Fig. 3.10D).

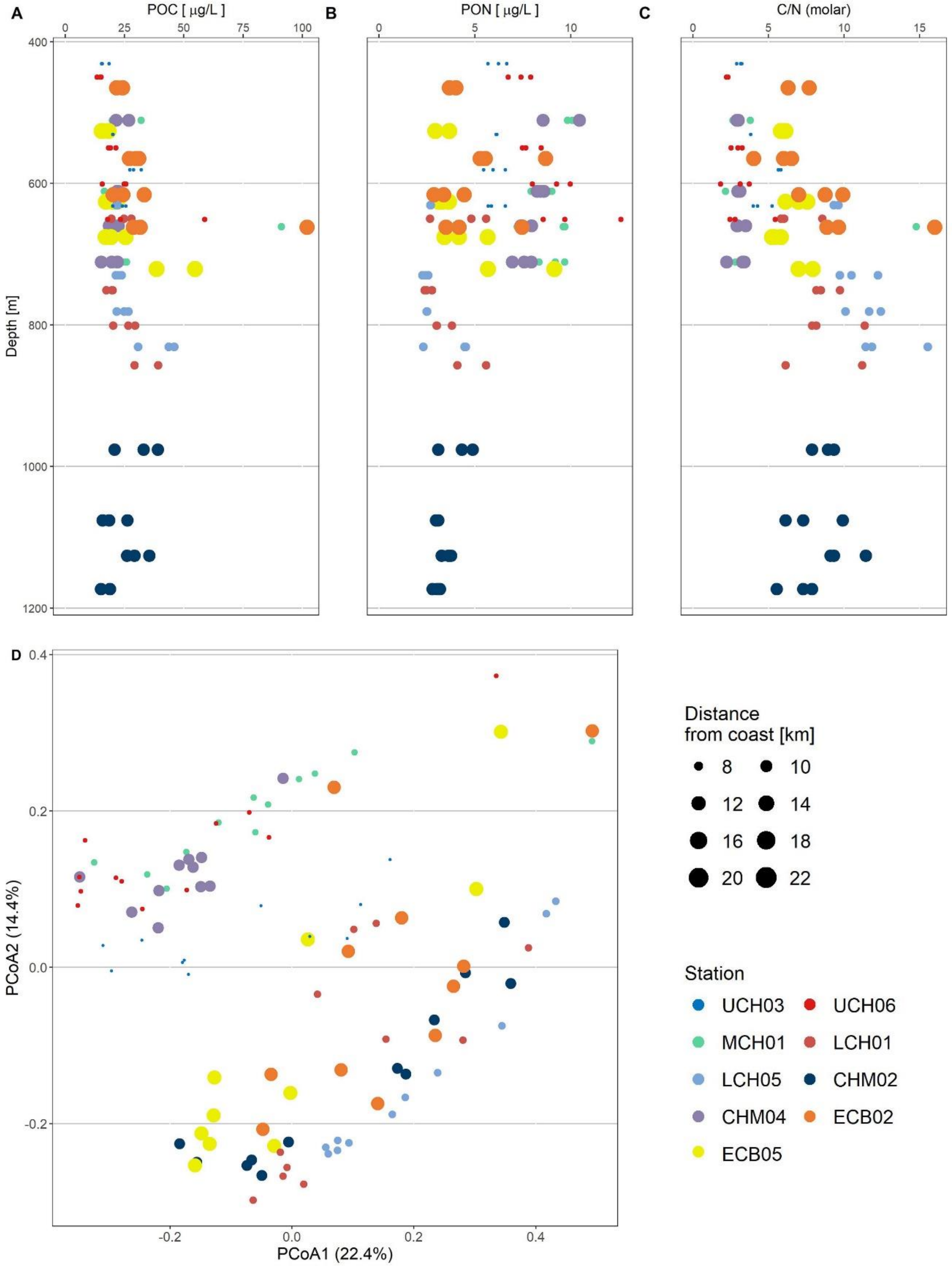


Figure 3.10. Particulate organic carbon (POC) (A); particulate organic nitrogen (PON) (B); molar C/N ratio (C) visualized colour coded by station and size dependent as distance from the coast. Principal coordinate analysis (PCoA) of data in the A, B and C (D).

3.4. Discussion

The current study had two aims. Firstly, to identify the water masses and characterize the SSC and nepheloid layer distribution in Blanes Canyon next to CWCs locations described in Chapter 2. Secondly, to characterize the immediate characteristics of a trawl induced BNL on a fishing ground passing through the canyon axis.

Water masses found in Blanes Canyon during the two cruises differed at the surface, where in February 2020 WIW was marginally present, while in January 2021 this water mass occupied the surface and sub-surface waters, displacing mAW, possibly further offshore beyond the across canyon transect. This can be related to dense shelf water formation processes taking place in the Gulf of Lions and subsequent displacement and cascading of the newly formed water masses (Millot, 1999). In the Gulf of Lions dense water is formed by winter convection processes (Millot, 1999). As the water masses gain density, they cascade down the slope and depending on the atmospheric and hydrodynamic forcings, this can result in WIW that settles between mAW and LIW or WMDW that is found below LIW (Vargas-Yáñez et al., 2012; Juza et al., 2019). Seasonal and interannual variability are important characteristics of WIW, which is clearly depicted in this study. Prevalence of WIW in the surface during 2021, showed a snapshot in WIW lifetime before cascading down to intermediate depths, above LIW where it is usually found (Millot, 1999; Vargas-Yáñez et al., 2012; Juza et al., 2019). During this movement, the WIW can potentially provide a pulse of fresh organic matter and potentially zooplankton to CWC communities, if it coincides with phytoplankton blooms (Pasqual et al., 2011; Thomsen et al., 2017). In the last 10 years there has been a noticeable decrease in frequency and intensity of dense shelf water cascading events and long-term impacts of these changes will be need to be studied in detail as they will influence the ecosystems and commercial fish species such as *A. antennatus* (Palanques et al., 2006a; Fabres et al., 2008; Sardà et al., 2009; Estournel et al., 2023).

The LIW was found at intermediate depths, while deeper areas were filled with WMDW. CWCs in Blanes Canyon were found in both water masses (Chapter 2). The LIW is often considered as a main pathway of coral distribution in the Mediterranean Sea (Freiwald et al., 2009; Taviani et al., 2011; Fabri et al., 2014; Chimienti et al., 2019; Wienberg et al., 2022). Firstly, the depth range of LIW coincides with geomorphic features characterized by hard substrate, such as seamounts and submarine canyons, which is known to be an important factor for coral settlement (Sartori, 1980; Taviani et al., 2005; Orejas et al., 2009; Bo et al., 2015; Cau et al., 2015). These geomorphic features are areas of complex hydrodynamics that include internal waves, upwelling, downwelling, dense shelf water cascading and storm induced sediment displacement, which can supply corals with organic matter from the surface (Duineveld et al., 2004; Mienis et al., 2007; Davies et al., 2009; Dodds et al., 2009). Moreover, along the isopycnals of front systems, i.e. the limits between different water masses or current systems, intermediate nepheloid layers (INL) are formed which retain organic matter and zooplankton (Puig et al., 2001; Fernandez-Arcaya et al., 2013). Another contribution to coral nutrition can come from the bottom nepheloid layer (BNL) that can vertically extend for several hundreds of meters (Mienis et al., 2007; Huvenne et al., 2011; Wilson et al., 2015b). Chapter 2 showed that CWCs are indeed found within the LIW, but also in the WMDW which is not often considered in CWC context, because many CWC studies in the West Mediterranean were focused on the upper slope (~ 500 m) where LIW is dominant (Orejas et al., 2009; Gori et al., 2013; Fabri et al., 2014; Grinyó et al., 2018; Dominguez-Carrió et al., 2022). As described above, WMDW is formed in Gulf of Lions from where it cascades down the slope, while mixing with the LIW, ultimately reaching the basin and settling as WMDW below LIW

(Millot, 1999). This could potentially mean that the WMDW can aid coral larvae transport to deeper parts of the basin. However, more studies are needed to clarify the role of WMDW in CWC life cycle.

More detailed insights from water samples collected in vicinity of CWCs highlighted a difference in organic matter characteristics between the canyon head (closer to the coast and shallower), compared to sites located further down the canyon head and east canyon branch (further form the coast). The results suggest that closer to the coast, particulate organic matter (POM) is fresher, based on higher PON and lower C/N ratio. This could potentially be explained by a downwelling event that brought fresh organic matter from the surface. Alternatively, settled fresh matter was resuspended in the BNL by bottom currents or internal waves (Zúñiga et al., 2009). Further down the canyon head, as depth increases, more degraded POM was found along with lower values of PON, which corroborates previous studies (Kiriakoulakis et al., 2011; Pasqual et al., 2011; Campanyà-Llovet et al., 2018). Lower POM and PON values which suggest lesser input of fresh matter, were also found in the east canyon branch, which is shallower but also furthest from the coast. That area is characterized by hemipelagic sedimentation processes from particles advected along-margin by the Northern Current, which may explain the degraded nature of the POM. Organic matter is slowly degraded as it is transported from the coast as well as though the water column.

The combined effect of frequency and intensity of high energy events and presence of fresh food may be an indicator to why colonial scleractinians prevail in the UCH (Chapter 2). Moreover, deeper down the canyon and in the ECB octocorals and black corals were predominantly found, where degraded food is mostly present as well as lack of lateral inputs from the continental shelf. Colonial scleractinians are considered to have higher energy requirements than octocorals and black corals, however due to lack of studies on latter two groups, it still remains to be confirmed (Maier et al., 2019a; Rakka et al., 2021; Derviche et al., 2022). Nevertheless, bearing in mind that our results are snapshots in a very dynamic environment prone to dramatic changes governed by high energy events, more studies are needed to understand better the role of different processes contributing to the availability and quality of POM with respect to CWCs on canyon walls.

The second aim of this study was to evaluate differences between the BNL during a fishing closure and immediately after a trawling event. The sampling after a trawler, was done during 2021, when COVID restrictions influenced the fishing activity in the area, by reducing it compared to previous years (Paradis et al., 2018) (Fig. 1.2). The lower activity in the area allowed to perform a targeted sampling immediately after a trawling event, amidst fishing boats. Our results showed that POC and PON values were several times higher after trawl passing. However, high C/N ratio which suggests that more degraded POM, was found both during fishing closure and after the trawl passage. While we cannot exclude the potential of contamination during sample preparation, it is possible that the fishing ground in the canyon axis is characterized by reworked, degraded sediment that cannot be replenished sufficiently during the fishing closure which only lasts for one month (Sañé et al., 2013; Paradis et al., 2019, 2021). Bottom currents can resuspend this sediment to the BNL, maintaining the characteristics of the fishing ground sediment. On the other hand, SSC was much higher during the trawling event, with a BNL extending up to 100 m from the bottom, reaching a maximum of 6 mg/L and reducing to 0.5 mg/L within 20 meters from the sea bottom. During times of full fishing potential, we can expect higher values than this, as it was shown for other nearby canyons (Arjona-Camas et al., 2019; Martín et al., 2014c). Such an enhanced BNL will probably stay in the canyon longer due to canyon topography and within-canyon dynamics. This suggests multiple impacts for CWCs living in the vicinity of the fishing ground: longer physical exposure to elevated SSC and dilution of fresh organic matter in large volumes of degraded POM.

High sedimentation and SSC has been shown to negatively impact coral physiology, including CWCs (Chapter 4). Studies have shown that sediment can cause injuries and tissue necrosis, feeding disruption and physiological stress (Brooke et al., 2009; Larsson et al., 2013b). Such a stress response may lead to increased energy allocation, with further impacts for coral physiology. Under these conditions, high availability of fresh, nutritious food is important. As a result, the presence of degraded POM may pose additional stressors on CWCs in Blanes Canyon. Further studies are needed to determine the effects of trawling impacts on CWC physiology.

4. CHAPTER 4: Vulnerability of six cold-water corals to sediment resuspension from bottom trawling fishing

4.1. Introduction

Technological improvements significantly expanded the depth limits of bottom trawling fishing since 1950s, allowing access to new fishing grounds below the mostly depleted shallower areas (Koslow et al., 2000; Morato et al., 2006; Victorero et al., 2018). Bottom trawling is the cause of the most extensive physical disturbance in marine environments (Eigaard et al., 2017; Amoroso et al., 2018; Kroodsma et al., 2018), with destructive impacts on megabenthic communities and high discard rates (Kelleher, 2005; Gilman et al., 2020). Growing understanding of environmental impacts of bottom-contact fisheries, especially bottom trawling, drove to the definition of Vulnerable Marine Ecosystems (VMEs) (Freiwald et al., 2004; FAO, 2009). These include cold-water coral (CWC) communities, composed of structurally complex, fragile, long-living and slow-growing species, especially vulnerable to diverse fishing gear impacts (Clark et al., 2016; Yoklavich et al., 2018; Pham et al., 2019; Angiolillo et al., 2021; González-Irusta et al., 2022). Recovery rates of CWCs after fishing closure have shown to be extremely slow, suggesting it may take decades to centuries to recover (Althaus et al., 2009; Huvenne et al., 2016; Clark et al., 2016; Morrison et al., 2020). Alongside direct destructive impacts, bottom trawling fishing resuspends large amounts of sediment into the water column due to ploughing and scraping of the heavy trawling gear, thus increasing suspended sediment concentration (SSC) over large spatial and temporal scales (Palanques et al., 2006b; Wilson et al., 2015a; Arjona-Camas et al., 2021). Moreover, resuspended sediment has a higher degree of degraded organic matter which can potentially affect benthic fauna (Pusceddu et al., 2014a; Wilson et al., 2015a; Paradis et al., 2022) (Chapter 2,3).

Long-term repeated and intensive bottom trawling taking place on the canyon flanks led to smoothing of canyon topography by dislodging large amounts of sediment to deeper parts of the canyon, mainly canyon axis, resulting in increased sedimentation rates (Canals et al., 2006; Puig et al., 2012; Paradis et al., 2018, 2020). At the same time, daily increases in SSC driven by bottom trawling fishing have been recorded various depths within canyons, demonstrating the effects of bottom trawling fishing, even outside the fishing grounds (Palanques et al., 2006b; Martín et al., 2014c; Wilson et al., 2015a; Arjona-Camas et al., 2019, 2021). Consequently, benthic communities that may be sheltered from the direct impacts of bottom trawling, are still exposed to the derived increased SSC, which can have harmful effects especially on suspension feeding sessile organisms (Larsson et al., 2013b; Kutti et al., 2015; Grant et al., 2019; Wurz et al., 2021) (Chapter 2,3).

CWCs are among several groups of species (e.g., sponges) that are known to increase structural complexity and habitat heterogeneity (Rossi et al., 2017). The ability to increase habitat heterogeneity lays with carbonate frameworks of colonial scleractinian corals (Scleractinia) and hydrocorals (Stylasteridae) or canopies of octocorals (Octocorallia) and black corals (Antipatharia) (Buhl-Mortensen et al., 2010; Roberts et al., 2016). Within and around CWCs, gastropods, crustaceans, echinoderms, fish, and many other species find shelter, feeding, and breeding grounds (Colloca et al., 2004; Buhl-Mortensen and Mortensen, 2005; Mastrototaro et al., 2010; Guilloux et al., 2010; Henry and Roberts, 2017; Linley et al., 2017; D'Onghia, 2019).

Major part of studies on the effects of increased SSC on corals have been focused on tropical species, being affected in their photosynthetic efficiency and growth rate, increased bleaching and tissue mortality, reviewed by Tuttle and Donahue (2022) (Tuttle and Donahue, 2022). Less studies have explored the effects of SSC caused by mine tailings, natural or artificial particles, on the widely distributed CWC *Lophelia pertusa* [now Desmophyllum *pertusum* (Addamo et al., 2016)]. According to this research, increased SSC drives to polyp blockage and mortality as well as physiological stress resulting in increased respiration, mucus production and decreased growth (Larsson et al., 2013b; Liefmann et al., 2018; Baussant et al., 2018, 2022).

However, there is a lack of information on the possible effects of increased SSC on other CWCs, such as other scleractinian species, octocorals and black corals. They are important contributors to benthic communities of the continental slopes, submarine canyons and seamounts, which are under pressure from bottom trawling (Fabri et al., 2014; Bo et al., 2015; Grinyó et al., 2018). This information is important, because the possible responses of different species to anthropogenic impacts may give some clues for understanding future seascapes based on these ecosystem engineering species (Rossi et al., 2017). In the Mediterranean submarine canyons, *Madrepora oculata* is the prevailing CWC, together with black coral and octocoral species, however there are still many unexplored areas (Gori et al., 2013; Fabri et al., 2014; Lastras et al., 2016; Arnaud-Haond et al., 2017; Orejas and Jiménez, 2019).

In this context, the aim of this Chapter is to assess the survival and physiological responses of six common CWCs in Mediterranean submarine canyons (*Dendrophyllia cornigera*, *Desmophyllum dianthus*, *Desmophyllum pertusum*, *Madrepora oculata*, *Leiopathes glaberrima* and *Muriceides lepida*) to increased SSC derived of reiterative bottom trawling activity. This was addressed performing a 9-month experimental study, where coral nubbins were regularly exposed, on week days, to increased SSC followed by a progressive decrease to background levels. The effect of SSC on CWCs were measured as survival, growth, respiration and excretion after 4 and 9 months of exposure.

4.2. Materials and methods

4.2.1. Coral collection, maintenance, and preparation

The CWCs *Desmophyllum dianthus* (100 polyps), *Desmophyllum pertusum* (6 colonies), *Madrepora oculata* (4 colonies), *Leiopathes glaberrima* (4 colonies) and *Muriceides lepida* (11 colonies) were sampled at 527 – 1165 m depth in the Blanes Canyon (NW Mediterranean Sea) with the ROV Liropus during the ABRIC-1 research cruise onboard the RV Sarmiento de Gamboa, in February 2020 (Table 4.1) (Chapter 2).

Table 4.1. Collection details of CWCs in the Blanes Canyon during the ABRIC-1 research cruise onboard the RV Sarmiento de Gamboa, in February 2020.

Latitude	Longitude	Depth (m)	*D. dianthus*	*D. pertusum*	*M. oculata*	*L. glaberrima*	*M. lepida*
41.605	2.864	559	x		x		
41.631	2.861	720	x		x		
41.629	2.861	564	x		x		
41.502	2.977	700	x				x
41.501	2.978	646	x			x	
41.501	2.979	596	x				x
41.497	2.979	650				x	
41.509	2.943	589	x				x
41.583	2.845	747	x	x			
41.524	2.842	1044	x	x			
41.528	2.856	740					x
41.528	2.856	742	x				
41.528	2.856	723					x
41.522	2.883	527	x				x
41.525	2.843	1165		x			
41.522	2.842	1014					x
41.522	2.842	1014	x				
41.522	2.842	942	x				x
41.581	2.843	758	x				x

After the sample collection, corals were maintained at 13 ± 0.2°C during the cruise in three 180 L aquaria, each connected to a chiller (TECO TK-2000) to control the temperature and a biological filter (EHEIM Classic 1500 XL) (Orejas et al., 2019). Water change was made every 2 days with seawater while no food was given to the corals during their maintenance onboard. Once on land, corals were transported (within 1 h) to the Experimental Aquarium Zone (ZAE) at the Institut de Ciències del Mar (ICM-CSIC) in Barcelona and kept in three 180 L aquaria in a thermally regulated experimental chamber, with continuous flow of 50 and 5 µm filtered Mediterranean seawater pumped from 15 m depth (Olariaga et al., 2009). Salinity ranged between 37.8 and 38.0 and water temperature was maintained at 12.0 ± 1.0°C by the thermally regulated experimental chamber and a supplementary chiller (TECO TK-2000) (Orejas et al., 2019).

Only specimens of the CWC *Dendrophyllia cornigera* were collected in the Cap de Creus Canyon (NW Mediterranean Sea) in 2006 and 2007 (see details in Orejas et al. 2011) and since then were maintained in ZAE at ICM-CSIC under the previously mentioned conditions. This species was included in the experiment as the specimens were available at the facility and, even though this species was not found during the ROV dives in the Blanes Canyon, its presence in this canyon has been confirmed by accidental caught by local fishermen (Ferran Martinez Olivero, pers. comm.). Indeed, it is an important representative of Mediterranean CWCs (Gori et al., 2014b; Castellan et al., 2019), commonly found in the submarine canyons in the northwestern Mediterranean (Orejas et al., 2009; Gori et al., 2013; Fabri et al., 2014; Lastras et al., 2016).

Corals were fragmented (except for *D. dianthus* which is a single polyp coral) and glued on glass supports (4 x 4 x 0.4 cm) using two-component epoxy putty (GROTECH Corafix® SuperFast). After coral nubbins preparation, the experiment was discontinued due to COVID-19 lockdown for 4 months. During this time and experimental period, coral nubbins were maintained under the previously mentioned controlled conditions and fed several times a day during the weekdays using a peristaltic pump. Food consisted of 40% crushed oily fish and derivatives of fresh white fish, 30% crustaceans, 25% various types of phytoplankton cultures, and the rest brine shrimp nauplius and additional aquaria supplements of vitamins, amino acids and stabilizers which was mixed and sieved at 40 µm. Each aquaria was supplied by 1 g of food per day, delivered by a peristaltic pump, 100 ml every 4 hours. After forced COVID-19 lockdown, coral nubbins that were in good shape (open polyps, intact coenosarc) were chosen for the experiment and haphazardly distributed in 15 experimental aquaria of 45 L each, with a continuous flow of fresh seawater at 13 L h^{-1} rate. Recirculating pumps (SICCE® Voyager Nano 2000) were put on the front wall of the aquaria, just above the bottom. Suspended PVC grids (15 x 24 x 1.5 cm grid size) were put in each aquarium 8 cm above the bottom, and two nubbins of each species were distributed evenly on the grid. The nubbins were positioned in an upright position, due to logistical constrains to keep them horizontal or facing downwards. This setup was chosen to facilitate syphoning settled sediment from the bottom of the aquaria at the end of each working day (Fig. 4.1). Corals were left for 2 weeks acclimating under the new conditions, before the beginning of the experiment.

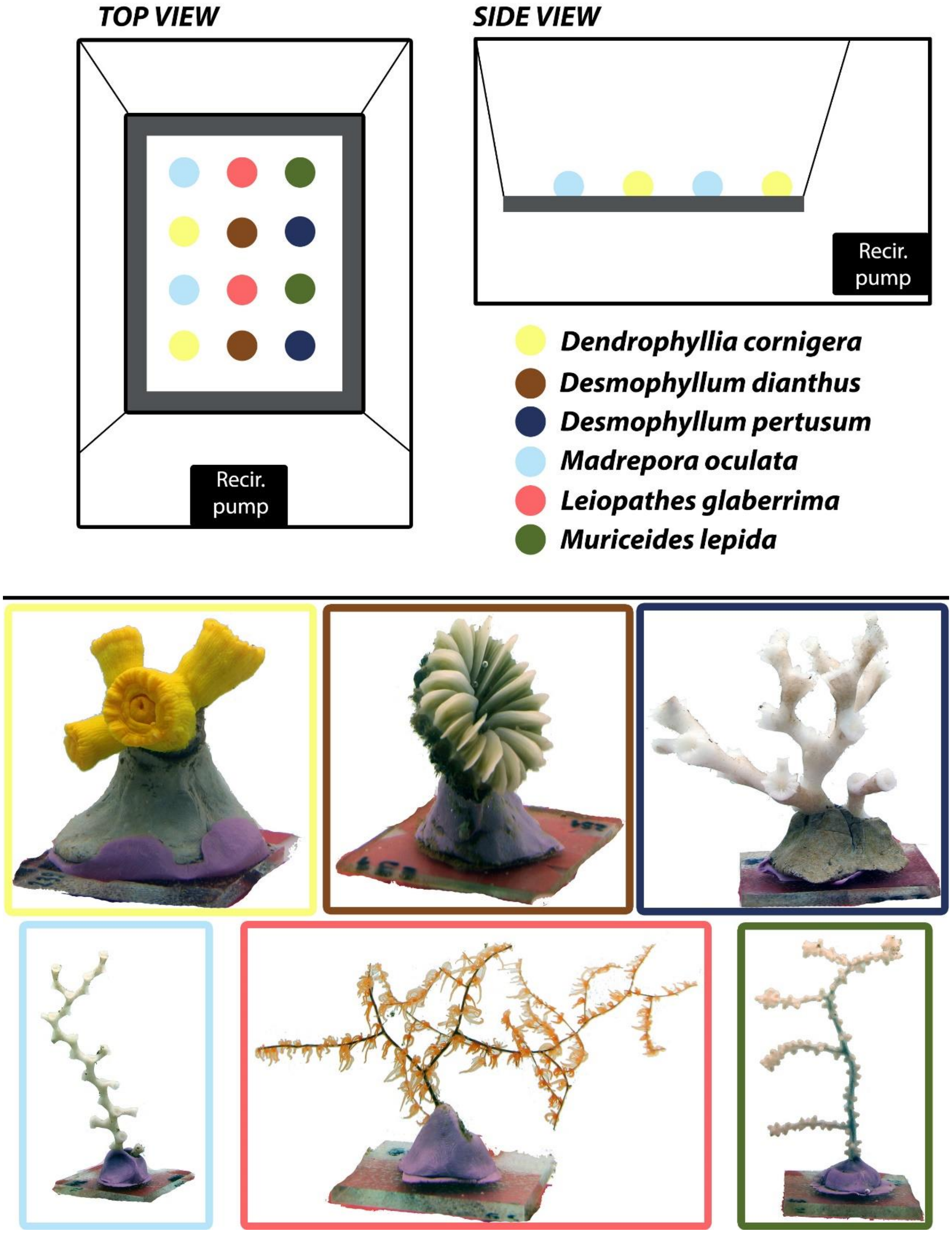


Figure 4.1 Experimental aquaria set up from top and side view, with colour coded coral species nubbins positioned the upright position on a PVC grid above recirculating pump.

4.2.2. Experimental setup

Coral nubbins were exposed to three contrasted treatments (5 aquaria each) for 9 months, a Control, a Low SSC and a High SSC treatment (Table 4.2), which were designed and adjusted prior to the start of the experiment.

Table 4.2. Summary of coral sizes used in the experiment. *D. cornigera*, *D. dianthus*, *D. pertusum*, *M. oculata* expressed in grams (g), while sized of *L. glaberrima* and *M. lepida* expressed in centimetres (cm). For each species Mean and Standard Deviation (SD) values are provided.

Species	Treatment	Size (g or cm)		Polyp number	
		Mean	SD	Mean	SD
Dendrophyllia cornigera (Lamarck, 1816)	Control	8.5	5.0	3.2	1.7
	Low SSC	9.7	4.0	3.3	1.7
	High SSC	10.0	7.1	3.8	3.7
Desmophyllum dianthus (Esper, 1794)	Control	10.6	5.3	1	0
	Low SSC	11.8	5.5	1	0
	High SSC	9.1	4.7	1	0
Desmophyllum pertusum (Linnaeus, 1758)	Control	7.9	3.0	17.1	9.2
	Low SSC	5.8	2.6	14.6	8.3
	High SSC	6.9	3.2	14.2	6.1
Madrepora oculata (Linnaeus, 1758)	Control	4.3	3.3	30.9	11.5
	Low SSC	3.3	1.8	33.9	8.2
	High SSC	3.2	1.6	33.5	9.8
Leiopathes glaberrima (Esper, 1792)	Control	41.9	25.9		
	Low SSC	51.0	28.2		
	High SSC	27.3	9.2		
Muriceides lepida (Carpine & Grasshoff, 1975)	Control	18.1	4.9		
	Low SSC	18.2	4.5		
	High SSC	18.6	6.7		

Sediment used in the experiment was collected using push cores mounted on the ROV *Liropus* during the ABIDES cruise on board the RV *Sarmiento de Gamboa* in September 2017. Upon collection, sediment cores were frozen and stored at -20ºC. Cores selected for the experiment come from several submarine canyons on the Catalan margin (Blanes, Arenys, Palamós and Francolí) from untrawled slope areas and canyon axis areas. The selected cores were freeze-dried and muffled at 450°C for 5 hours to remove organic matter. Clumps of sediment were gently crushed to facilitate suspension in a slurry, before adding the sediment to the experimental aquaria. Sediment grain size was analysed using the top two centimetres of six core samples using Horiba Ltd. Partica LA-950V2m particle size-analyser, resulting in average 83.5 ± 5% of silt and 16 ± 5 % of clay.

Turbidity monitoring in the experimental aquaria was preformed using a turbidity logger (AQUAlogger® 210TYPT from AQUATEC) on regular bases during the experiment. Conversion from turbidity (FTU) to suspended sediment concentration (SSC, mg L^{-1}) was established based on water samples taken at 10 increment turbidity values. Seawater samples (0.5 – 1 L) were filtered on pre-weighted Nuclepore 0.4 µm filters. Afterwards, they were dried for 48 h at 40°C and measured using a 0.01 mg resolution balance (Sartorius, BP210D model). The obtained linear relationship (SSC = 0.74 * FTU - 0.11) is in range with previous studies for the western Mediterranean (Guillén et al., 2000; Arjona-Camas et al., 2021). Sediment was gently added to the experimental aquaria for the two increased SSC treatments every weekday morning, and not during weekends to mimic the trawling activity schedule, closing the water inflow for 1 h after adding the sediment. The SSC temporal evolution of the treatments was characterized by a sharp increase, followed by a gradual decrease towards background SSC levels, which were reached within 6 hours (Fig. 4.2). In the Control treatment no sediment was added, and the SSC was maintained at average 0.5 ± 0.45 mg L^{-1}. In the increased SSC treatments, the initial maximum average was 6.7 ± 1.9 mg L^{-1} for the Low SSC treatment and 38.1 ± 3.8 mg L^{-1} for the High SSC treatment, before letting it slowly decreasing to the background SSC levels (Fig. 4.2). The exposure to suspended sediment was designed to simulate bottom trawling-induced turbidity, as detected with instrumented moored observations in submarine canyons flanks on the Catalan margin (Martín et al., 2014c).

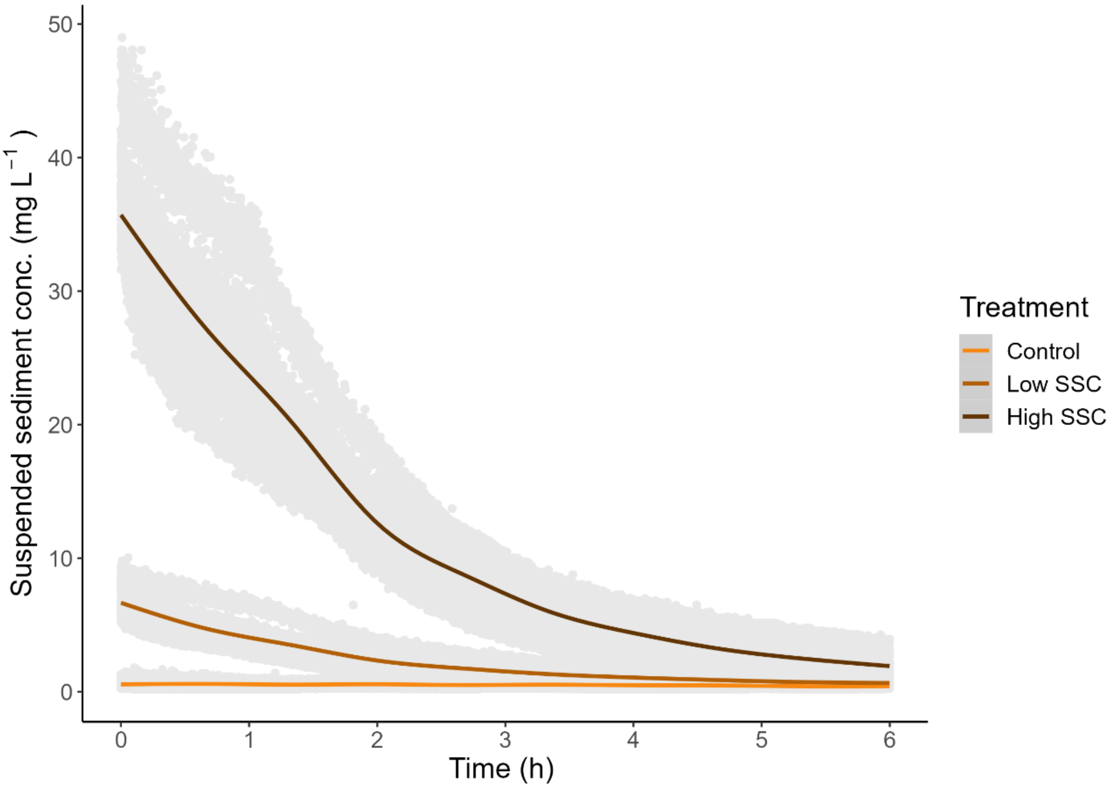


Figure 4.2. Turbidity profiles in the three experimental treatments converted to suspended sediment concentration (SSC) based on the obtained linear relationship (SSC = 0.74 * FTU - 0.11), n = 48.

4.2.3. Coral mortality

Mortality was assessed at the end of the experiment, by comparing number of live polyps at the beginning and end of the experiment for scleractinian species, or by comparing live tissue length for the octocoral and the black coral. Mortality is reported as % (average ± standard deviation).

4.2.4. Coral growth

Weight of the scleractinian nubbins were determined by the buoyant weight technique (Jokiel et al., 1978) using a 0.1 mg resolution balance (Mettler Toledo® AB204 SFACT). All the nubbins were weighted before the start of the experiment, as well as after 127, 203 and 280 days. Skeletal density values for the scleractinian species were taken from previous studies (Movilla et al., 2014a, 2014b). Live tissue length of black coral and octocoral nubbins was measured as the length of the branches covered by live tissue using photogrammetry (Fig. 4.3). The setup included a waterproof servomotor (Steplab, Italy) with a supporting platform which was set in the middle of a well-light 30 L aquarium (Fig. 4.3A). Each nubbin was put in the middle of the slowly rotating platform and photographed with an 18-megapixel resolution digital camera (Canon EOS Kiss X7) located in front of the aquarium. Images were acquired after 30 days from the start of the experiment, and again after 127 and 280 days. Photogrammetry 3D reconstruction of each nubbin was performed in AgiSoft Metashape Professional version 1.7 (AgiSoft PhotoScan Professional, 2021). The workflow included: adding photos (Fig. 4.3B), adding masks where necessary for keeping only the coral nubbin visible for reconstruction (Fig. 4.3C), identifying markers and setting scale bars (Fig. 4.3D), producing a dense point cloud (Fig. 4.3E), and measuring length of branches covered by live tissue using polyline tool (Fig. 4.3F). The error of the measurements is given in section 4.3. Usually, 40 photos per nubbin were sufficient for reconstruction (Fig.4.3G-L). The dense point cloud was used for measurements as it was easier to trace the branches and we were able to correct for different stages of polyp retraction in case of *M. lepida*. Live tissue length was traced manually along the branches and then summed together for each nubbin.

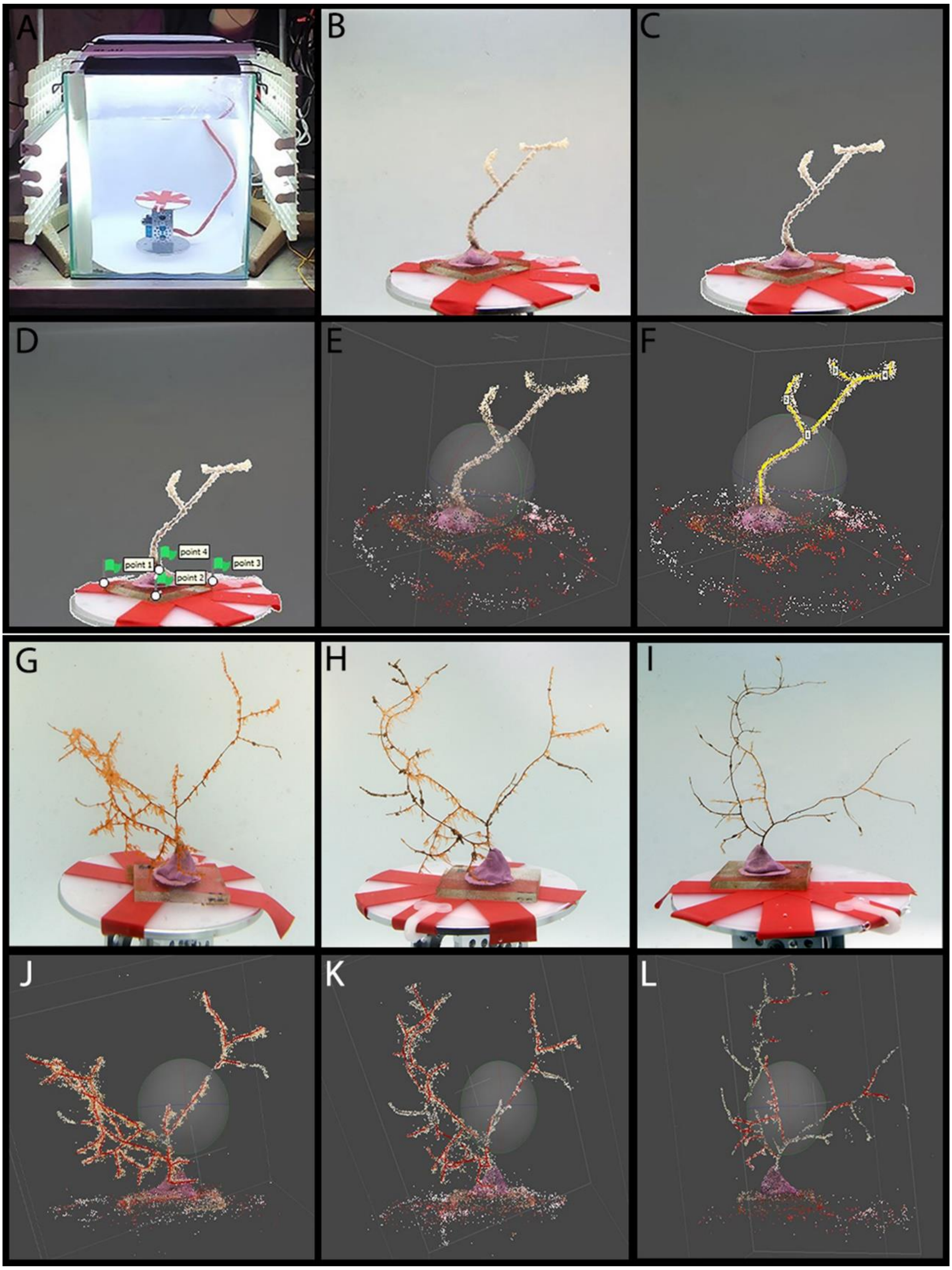


Figure 4.3. Photogrammetry setup and workflow. Laboratory set up including well-light 30 L aquarium and servomotor (A); Workflow in Agisoft Metashape: add photos (B); create and apply masks (C); set markers and scale bars (D); dense point cloud (E); track polyline along the dense point cloud (F); *Leiopathes glaberrima* photos and reconstructions after 1 month (G,J); 5 months (H,K); and 9 months (I, L).

For each coral nubbin, growth rate was calculated as the slope of linear regression using logarithmically transformed weight (scleractinian) and live tissue extension (black coral and octocoral) data and reported as % d^{-1} (average ± standard deviation).

4.2.5. Coral metabolism

Short-term incubations to assess coral respiration and excretion rates were preformed after 105 – 121days (4 months) and 231 – 254 days (8 – 9 months) of sediment exposure. Two water baths were prepared in order to maintain temperature constant during incubations. Each was equipped with a submergible magnetic stirrer, providing space for a total of 24 glass vials at a time. Since there were 180 nubbins (2 nubbins per species (6) per aquaria (15)) it took approximately 20 calendar days to conclude the metabolic incubations for all coral nubbins. The day before the incubation, coral nubbins were put in a separate aquarium where they were not fed for 24h. For the incubation, coral nubbins were put individually in glass vials 380–1200 ml in volume, depending on the species, i.e., for *D. dianthus* nubbins 380 ml vials were used and for several large *L. glaberrima* nubbins 1200 ml vials were used. The vials were filled with filtered (1 µm) seawater at 12°C, with a Teflon coated magnetic stirrer inside insuring constant water movement during the incubation. Before the beginning of each incubation, dissolved oxygen was measured with an optical instrument (YSI™ ProODO) and 20 ml of seawater (filtered by 0.2 µm) were taken for the initial determination of ammonium concentration. Each vial was manually closed with rubber band and a gas impermeable plastic foil. Each incubation lasted for 15 h and temperature was kept stable at 12 ± 0.1°C during this time. Glass vials with no coral inside were used as controls during the incubations. At the end of the incubation, dissolved oxygen was measured, and 20 ml of seawater (filtered by 0.2

µm) were taken from each vial for the determination of the final ammonium concentration. Oxygen consumption was calculated from the depletion over time of dissolved oxygen concentration in each vial, subtracting the change measured in the control vials. Ammonium concentration was determined immediately after each incubation using a nutrient analyser (AA3 HR Seal Analytical with Fluorometer Jasco). Ammonium production was calculated as the increase over time of ammonium concentration in each vial, subtracting the change measured in the control vials. Coral respiration and excretion were standardized by weight for scleractinian nubbins, and live tissue length for black coral and octocoral nubbins. Respiration is reported as µmol O_2 g^{-1} d^{-1} (average ± standard deviation) for the scleractinian corals, and µmol O_2 cm^{-1} d^{-1} (average ± standard deviation) for the black coral and octocoral, whereas excretion is reported as µmol NH_4 g^{-1} d^{-1} (average ± standard deviation) for the scleractinian corals, and µmol NH_4 cm^{-1} d^{-1} (average ± standard deviation) for the black coral and octocoral.

4.2.6. Statistical analyses

Data exploration, statistical analyses and graphical presentation were done with R 4.0.1 (R CoreTeam 2022), following Crawley (2013) and Zuur et al. (2009) (Crawley, 2013; Zuur et al., 2009). The experimental design is a hierarchical one, which implies data dependency, more specifically each treatment consisted of 5 aquaria within which two nubbins of each species were present. In order to represent this dependency, we aimed at using generalized linear mixed effect model (*lm4* package) (Bates et al., 2015) with coral code (individual coral nubbin) and aquaria as random effects. In cases where this model design was too complex for the data used, we chose the prevailing random effect (see below). Data analysis was performed by comparing treatments for each species separately.

Mortality data were analysed using generalized linear mixed effect models with aquaria as a random effect. Binomial distribution was used for colonial scleractinian corals (*D. pertusum*, *M. oculata* and *D. cornigera*) appropriate for count data (live polyp number). In case of *D. cornigera*, we removed the control from the statistical analysis as it has a uniform response (no mortality). In case of *L. glaberrima*, we used generalized linear mixed effect models with binomial distribution, appropriate for proportion data (percentage of mortality). For *D. dianthus* there was no mortality in any of the treatments, while for *M. lepida* only one nubbin showed mortality (loss of tissue). These data were not analysed statistically.

Growth, respiration and excretion rate data were analysed using linear mixed effect models (*lm4* package, Bates et al., 2015) including an interaction between time and treatment as fixed factors, and coral code as random factor. Including aquaria effect as a random effect was considered alongside coral code in order to account for multiple coral nubbins in the same experimental aquaria, but data collected could not support such a complex model (e.g., not enough replicates per species per tank to handle the dependencies (aquaria and coral codes)). On the other hand, including only “aquaria” as a random effect proved to be insufficient, therefore we only used “coral code” as a random factor in all models to account for repeated measures. Diagnostic checking was aided by *lmtest* package (Zeileis and Hothorn, 2002), while model diagnostics performed in *DHARMa* package (Hartig, 2022), designed to handle complex linear mixed effect models.

4.3. Results

Average and standard deviation of scale bar error used in photogrammetry reconstruction of corals was 0.079 ± 0.066 cm. Oxygen and ammonium values in coral incubations ($t = 56.04, p < 0.001$; $t = 30.56, p < 0.001$) were significantly different from blank incubations ($t = - 32.70, p < 0.001$; $t = -14.86, p < 0.001$) running at the same time. Coenosarc deterioration and sediment ingestion were not evaluated in this study, but both were observed, especially in the SSC treatments. Polyp behaviour during the experiment was not evaluated, however during the metabolic incubations we observed similar *L. glaberrima* polyp reactions as in Ruiz-Ramos et al. (2017), such as mucus strains, contracted, swollen and disintegrating polyps, as well as sweeper tentacles.

4.3.1. Coral mortality

Mortality was observed in all species except for *D. dianthus* and marginally in *M. lepida*, where only one fragment in the Low SSC treatment lost some tissue at the end of the experiment (Fig. 4.4). *Dendrophyllia cornigera* showed low mortality with no differences among treatments (Fig. 4.4, Appendix B). *Desmophyllum pertusum* showed significant increase in polyp mortality in the increased SSC treatments when compared to the control treatment, but no differences between the two SSC treatments (Fig. 4.4, Appendix B). Mortality of *M. oculata* was observed in all treatments, but a significant increase was observed in the increased SSC treatments compared with the control treatment, but no differences between the two SSC treatments (Fig. 4.4, Appendix B). *Leiopathes glaberrima* showed mortality as tissue loss in all treatments, with no statistical differences among treatments (Fig. 4.4, Appendix B).

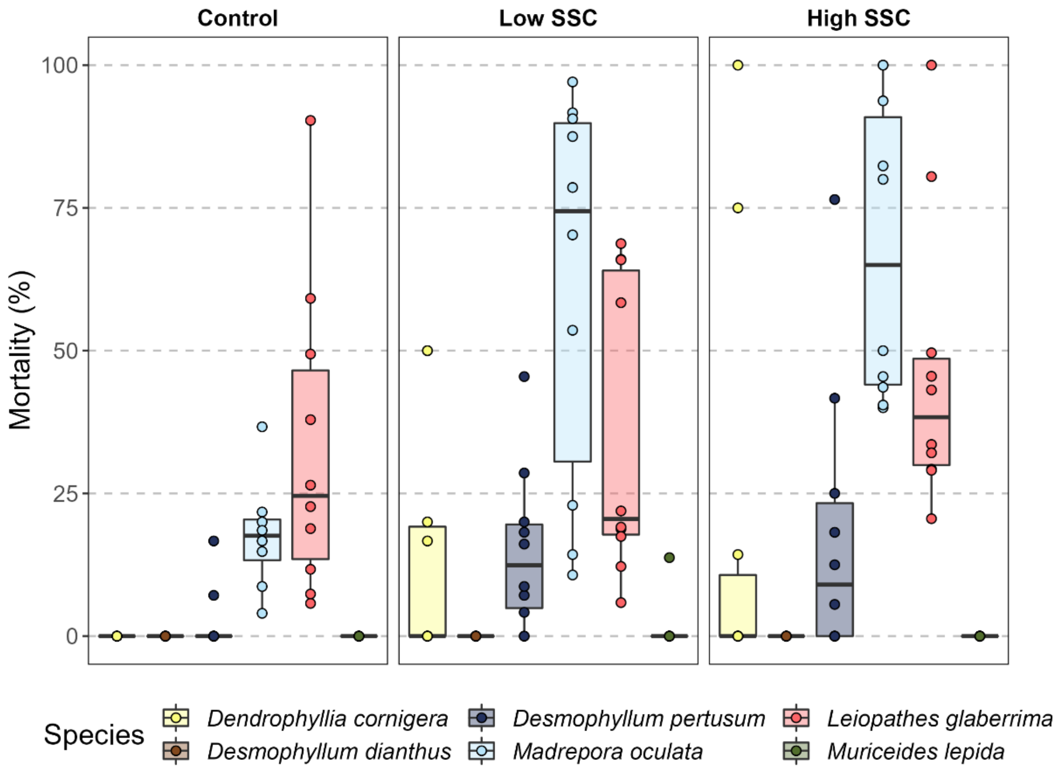


Figure 4.4. Mortality of the studied CWC species with increasing suspended sediment concentration (SSC) over the 9-month period, expressed as polyp mortality for the scleractinian species (*D. cornigera*, *D. dianthus*, *D. pertusum* and *M. oculata*) and tissue loss for the black coral (*L. glaberrima*) and the octocoral (*M. lepida*).

4.3.2. Coral growth

Except for *L. glaberrima*, which experienced only tissue loss, all species grew over the course of the experiment (Fig. 4.5, Appendix B). Neither of the increased SSC treatments showed statistically significant impact on growth rates of the studied species (Appendix B).

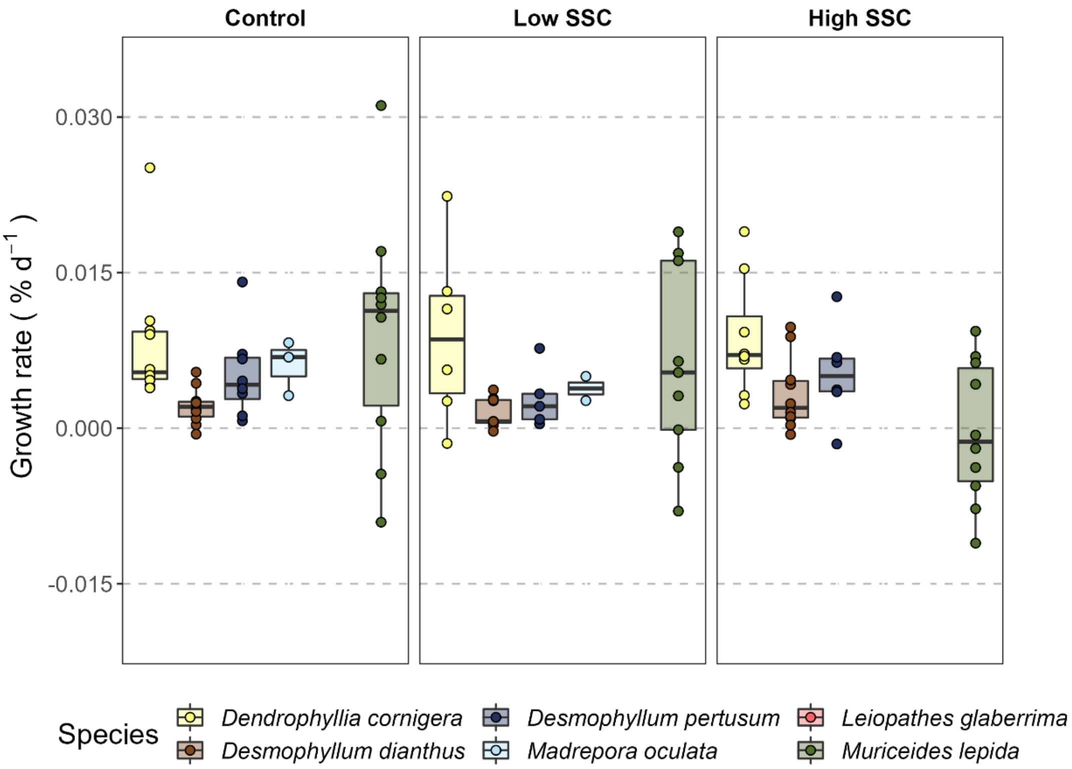


Figure 4.5. Growth rate of the studied CWC species with increasing suspended sediment concentration (SSC) over the 9-month period.

4.3.3. Coral metabolism

4.3.3.1. Respiration

All species showed a decrease in respiration with time, whilst the effect of increased SSC varied between species. *Dendrophyllia cornigera* and *D. dianthus* did not show any significant differences in respiration after 4 and 9 months, and no differences among treatments (Fig. 4.6, Appendix B). *Desmophyllum pertusum* showed a significant interaction between time and High SSC treatment on respiration, with highest respiration after 4 months and lowest respiration at the end of the experiment (Fig. 4.6, Appendix B). *Madrepora oculata* showed a significant effect of time on respiration, with a significant decrease in respiration from 4 to 9 month in all the treatments. Moreover, a significant effect was detected on the interaction of time and Low SSC treatment, while this was not investigated for the High SSC treatment as there were no nubbins with less than 15 % mortality at the end of the experiment in this treatment (Fig. 4.6, Appendix B). *Leiopathes glaberrima* showed no significant differences in respiration with time and treatment (but the lack of any nubbin with less than 15 % mortality made it impossible to statistically evaluate the effect of time in the High SSC treatment) (Fig. 4.6, Appendix B). *Muriceides lepida* showed a statically significant decrease of respiration with time in all the treatments (Fig. 4.6, Appendix B).

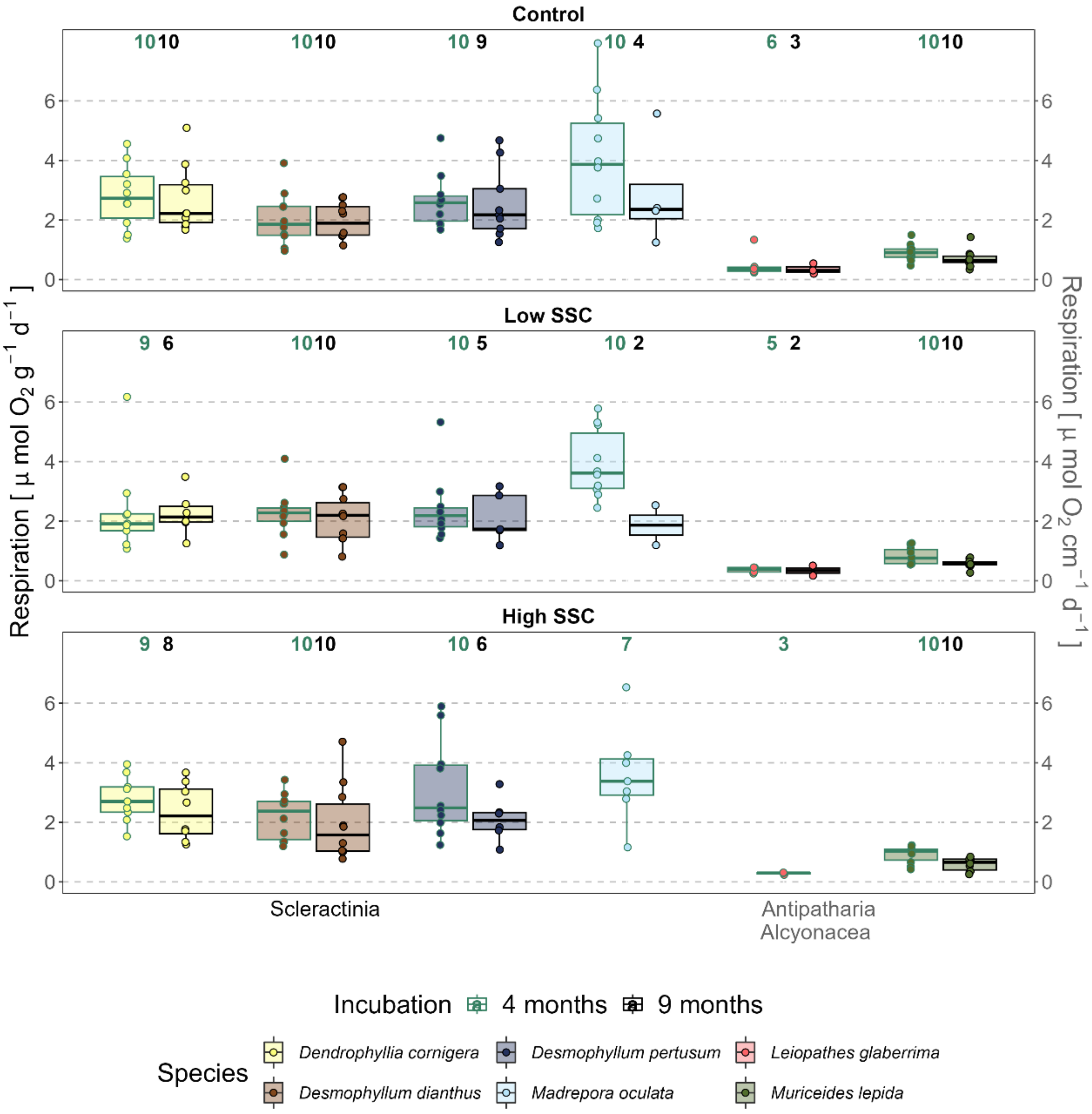


Figure 4.6. Respiration rate of the studied CWC species with increasing suspended sediment concentration (SSC) over 4-month (orange line) and 9-month period (black line). Number of nubbins with less than 15% mortality at each incubation is noted above the box plot.

4.3.3.2. Excretion

Dendrophyllia cornigera and *D. dianthus* did not show any significant differences in excretion after 4 and 9 months, and no differences among the three treatments (Fig. 4.7, Appendix B). *Desmophyllum pertusum* showed statistically significant interaction of time and Low SSC treatment, as well as for each factor separately (Appendix B), with a significant decrease in excretion with time in Low SSC treatment, and the highest excretion values observed after 4 months. On the other hand, the Control and High SSC treatment showed a significant increase in excretion with time (Fig. 4.7). Excretion did not change in *M. oculata* with time, and under the three treatments (but the lack of any nubbin with less than 15 % mortality made impossible to statistically evaluate the effect of time in the High SSC treatment) (Fig. 4.7, Appendix B). *Muriceides lepida* showed a significant decrease in excretion with time in all treatments (Fig. 4.7, Appendix B), and the Low SSC treatment significantly different from the Control and the High SSC treatments (Fig. 4.7, Appendix B).

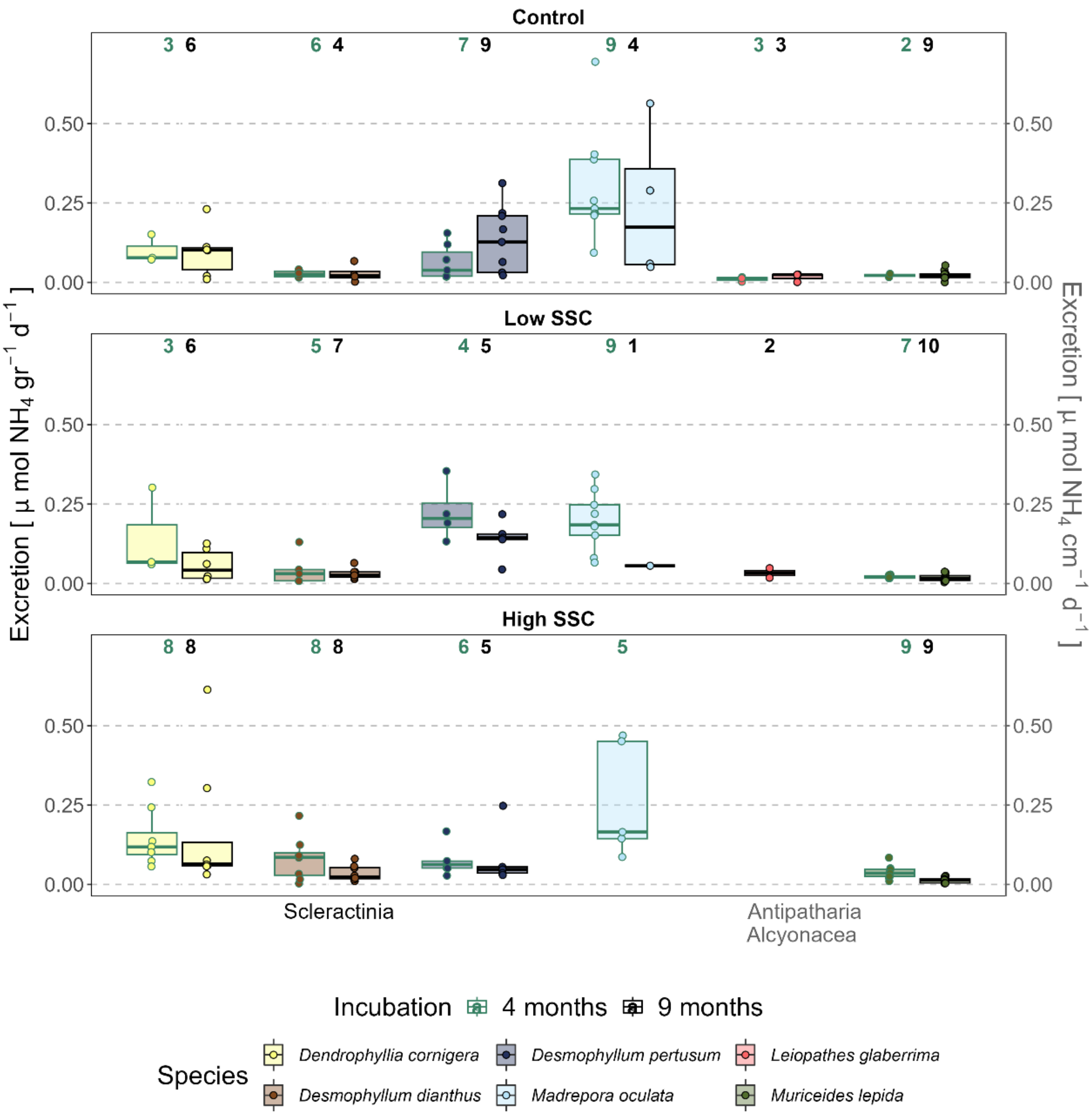


Figure 4.7. Excretion of the studied CWC species with increasing suspended sediment concentration (SSC) over 4-month (orange line) and 9-month period (black line). Number of nubbins with less than 15% mortality at each incubation is noted above the box plots.

4.4.Discussion

This study examined the effect of increased turbidity caused by natural sediment on survival, growth and physiology of six common CWCs found in the Mediterranean Sea. The results showed species-specific responses to increased turbidity.

4.4.1. Species-specific response

After 9 months of repeated exposure to daily increase in SSC from natural sediments, colonial scleractinian corals were significantly impacted. More specifically, *D. pertusum* showed average of 16 ± 19% mortality in SSC treatments, and *M. oculata* an average of 64 ± 29% in the same conditions. Previous studies exploring the effects of SSC on *D. pertusum* showed high variability in response to different concentrations and type of sediment, as well as duration of sediment exposure, but a general trend of increased mortality with increased SSC is common (Brooke et al., 2009; Larsson et al., 2013b; Baussant et al., 2022). Brooke et al. (2009) found that after 14 days of repeated exposure to suspended natural sediments, *D. pertusum* experienced higher mortality with increasing SSC. More specifically, at 54 mg L^{-1} polyp mortality was < 20% while at 103, 245 and 362 mg L^{-1} mortality was > 50%, > 70%, close to 100%, respectively. Larsson et al. (2013b) found lower mortality rates of *D. pertusum* after 3 months of continuous exposure to 25 mg L^{-1} of natural sediment (0.3% polyp mortality) and drill cuttings (2.2% polyp mortality). On the other hand, Baussant et al. (2022) exposed *D. pertusum* to suspended drill cuttings (4, 14, 19 and 49 mg L^{-1}), or barite (12, 26, 63 mg L^{-1}) and bentonite (11, 23, 48 mg L^{-1}) particles for 4 hours/day for 5 days, followed by a recovery period. High polyp mortality was observed when exposed to high SSC, with variability ranging from 20 – 70% polyp mortality. However, no mortality was observed in SSC treatments with drill cuttings that included repeated cycles of just 1h pulse, followed by 2h resting period reaching SSC peaks of 2, 12 and 52 mg L^{-1} over 12 weeks, followed by a 14-week recovery period (Baussant et al., 2018). Taking into account that in mentioned experiments, the sediment used was not associated to an organic matter content, the mere presence of inorganic particles in different concentrations interferes with the survivorship of this species. This is in line with the fact that an abundant but not digestible potential food source is a key factor to understand suspension feeding species distribution and mortality.

Compared to *D. pertusum*, *M. oculata* appears to be more sensitive to the effects of SSC, according to the findings in this study. This difference might be due to different internal morphologies of the two corals. Microtomography (micro-CT) analysis and decalcification methods (Lartaud et al., 2019; Fabri et al., 2022) showed that *D. pertusum* polyps are connected among calyxes by connective tissue which could provide an advantage by sharing nutrients between polyps. *M. oculata* has clear calcified separation between calyxes (Lartaud et al., 2019; Fabri et al., 2022), effectively being able to communicate among polyps only by coenosarc, a thin tissue layer covering coral skeleton. This coenosarc can be easily damaged by sediment abrasion or anoxic conditions created by accumulated sediment (Larsson and Purser, 2011; Allers et al., 2013). While *D. pertusum* has shown to be efficient in sediment removal with a specific mechanism (i.e., mucus production, Larsson and Purser, 2011), the degree of efficiency of sediment removal is unknown for *M. oculata* and other species. Without connection among polyps, every polyp of *M. oculata* is isolated if coenosarc is damaged by sediment and distal to the damaged area polyps cannot feed the affected ones. As a result, long-term exposure to SSC may exhaust lipid storage used by the coral to increase mucus production in the most exposed polyps. An *in situ* growth experiment confirmed *D. pertusum* and *M. oculata* vulnerability to sediment exposure in a submarine canyon, where both species showed high mortality after 15 months exposure to high sediment coverage as a results of a dense water cascading event (Lartaud et al., 2017).

While mortality was a prominent response to SSC, growth, respiration, and excretion of *D. pertusum* and *M. oculata* did not show significant changes due to sediment exposure in this experiment.

Lack of significant effect of turbidity on CWC physiology has been similarly reported (Larsson, et al., 2013b; Baussant et al., 2018, 2022), suggesting that other factors such as temperature and food quality and quantity play a stronger role on basic metabolic functions of corals (Naumann et al., 2011; Larsson et al., 2013a). In the study by Larsson et al. (2013b) respiration rates increased over the course of 3 months both in coral exposed and not exposed to sediment, while growth did not show significant differences among treatments, although lower growth rates were found in corals exposed to high sediment concentrations. These results were attributed to the high food supplied to corals in this experiment (Larsson et al., 2013b), since other studies providing less food found lower growth and respiration rates (Baussant et al., 2018, 2022). Another study showed that the lack of food in passive suspension feeders is a key factor to understand reproductive output and the capability to store energy (Gori et al., 2014a). Even if CWCs feed on different types of food, from dissolved and particulate organic matter to phytoplankton and zooplankton (Duineveld et al., 2004, 2007; Carlier et al., 2009; Dodds et al., 2009; Mueller et al., 2013; Gori et al., 2014a; Maier et al., 2019b; Rakka et al., 2019) and can withstand long periods of food deprivation (Naumann et al. 2011; Larsson et al., 2013a), the sediment interference may be excessive for their metabolism, provoking changes in their eco-physiological response.

Based on these findings, the low metabolic rates of *D. pertusum* and *M. oculata* in our study compared to previous experiments (Naumann et al., 2014; Maier et al., 2019b), could be related to the lack of zooplankton in their diet over the course of the experiment (Naumann et al., 2011) or ingestion of inedible sediment particles. Compared to previous results, this may suggest a potential interaction between food availability, and coral resistance to SSC. When abundant food is available, coral metabolism is increased and lipid reserves replenished (Gori et al., 2014a), which leads to effective protection against low SSC in form of increased mucus production, ciliary movement, and growth rate. Conversely, when food is reduced, such as in present study, coral metabolism is low and exposure to SSC may result in polyp mortality. This could be of high importance, due to the forecasted reduction in food availability in the deep sea, because of the ongoing global change (Sweetman et al., 2017; Henson et al., 2022), and will need further investigations. Low respiration and excretion rates also observed for *D. cornigera*, compared to previous studies (Gori et al., 2014b; Reynaud et al., 2021), also support that limited food was available to corals in the experiment, resulting in (low) polyp mortality induced by SSC in a species that has shown acclimation to increased temperature and reduced pH, when abundant food is available (Naumann et al., 2013; Movilla et al., 2014b; Gori et al., 2014b; Reynaud et al., 2021).

In contrast to the studied colonial scleractinian CWC, the solitary *D. dianthus* and the gorgonian *M. lepida,* showed resistance to exposure to both low and high SSC in present experiment. This finding endorses the idea of a metabolic flexibility of *D. dianthus*, based on previous studies (Naumann et al., 2011; Maier et al., 2021; Beck et al., 2022). This means the species can react relatively fast to changing environmental conditions to support basic functions. Acclimation to reduced pH has been shown in *D. dianthus* (Carreiro-Silva et al., 2014; Beck et al., 2022), where metabolism is affected by food availability and temperature (Naumann et al., 2011; Gori et al., 2016). Results of the study suggest that, even under reduced food availability, *D. dianthus* can probably efficiently remove large quantities of sediment from its surface, with apparently no effects on its metabolism. This capacity may contribute to explain the cosmopolitan distribution of *D. dianthus*, also thriving in high-sediment environments such as fjords (Försterra and Häussermann, 2003) and submarine canyons (Fabri et al., 2014)(Chapter 2).

To our best knowledge, present results are the first for the gorgonian *M. lepida*. Along with *D. dianthus*, this species showed no mortality neither change in respiration and excretion when exposed to SSC. The elastic and flexible gorgonian skeleton enables bending of the colony in response to external forces (e.g., currents) which aids sediment removal, without spending coral energy. The deep sea gorgonian *Primnoa resedaeformis* (Gunnerus, 1763) and the soft coral *Duva florida* (Rathke, 1806) exposed to glass beads and mine tailings (8 and 18 mg L^{-1}) showed a similar polyp survivorship (Liefmann et al. 2018). A reduced food input due to polyp retraction was observed for *D. florida*, and tissue abrasion in *P. resedaeformis* (Liefmann et al., 2018). In the present experiment, *M. lepida* did not show coenenchyma (tissue) loss, but a form of overall contraction or shrinkage in nubbin size with increasing SSC, although not significantly different. This form of contraction or shrinkage of the whole nubbin, instead of loss of branches or tissue as observed in other studies (Rossi et al., 2011), should be further explored as a possible strategy for gorgonians to cope with high-turbidity or being more generally related to unfavourable conditions.

Unlike all the other studied species, *L. glaberrima* showed high mortality rates in all treatments, including the control at the end of the experiment. This species has shown difficult to maintain in laboratory over long periods of time (Orejas et al., 2019), and only short experiments were conducted to explore the effects of oil and dispersants on the physiology of the species (DeLeo et al., 2016; Ruiz-Ramos et al., 2017). In the current study, we observed similar responses as in Ruiz-Ramos et al. (2017), such as mucus strains, contracted, swollen and disintegrating polyps. Alongside, sweeper tentacles were often seen, especially in the orange morph, perhaps assuming a defensive role. Based on our observations during the experiment, we hypothesize that lower current and smaller sized food particles may be more appropriate for maintaining this species in laboratory (Orejas et al., 2019).

4.4.2. Ecological consequences

Submarine canyons are important and common geomorphological features, especially in the Mediterranean Sea (Harris and Whiteway, 2011; Fernandez-Aracaya et al., 2017). They are main pathways of water and particles transport from shallow to deep waters, as well as areas of increased productivity, biodiversity, and biomass (Canals et al., 2006; De Leo et al., 2010; Puig et al., 2014; Fernandez-Arcaya et al., 2017). CWCs are often found thriving in submarine canyons that provide adequate substrate, flow and food (Orejas et al., 2009; Gori et al., 2013; Fabri et al., 2014), especially in the Mediterranean Sea (Puig and Gili, 2019). Steep canyon environments are not subjected to direct impacts of bottom trawling, as fishing gear would get easily entangled in rocky walls and overhangs. However, sediment resuspended by bottom trawling on canyon flanks and rims can travel long distances through the canyon (Martín et al., 2014c; Arjona-Camas et al., 2019, 2021), potentially impacting the benthic fauna living on the canyon walls.

From this study, bottom trawling fisheries may indirectly affect - due to increased SSC - two colonial scleractinian corals found in Mediterranean submarine canyons, *D. pertusum* and *M. oculata*, i.e., two species currently endangered in the Mediterranean Sea (Otero et al., 2017) and predicted to reduce their distribution due to climate change (Maier et al., 2019a). Alongside, predicted reduction in food availability would further increase their vulnerability (Campanyà-Llovet et al., 2017), reducing their energy reserves which will decrease their cleaning mechanisms, such as mucus production. Reduction in colonial scleractinian abundance will reduce associated diversity and abundance. *Desmophyllum pertusum* and *M. oculata* are important contributors to benthic communities as they provide shelter, feeding grounds and nursery areas for many species within and around their three-dimensional complex skeletons (Roberts et al., 2006; D'Onghia, 2019). This study has shown the importance of including indirect effect in spatial management as it can have long term effects(Tiano et al., 2019; Downie et al., 2021; Tsikopoulou et al., 2022). On the other hand, increased SSC coming from bottom trawling, may be favouring resistant species such *D. dianthus* and *M. lepida*, more prone to resist a shortage in available food than the other species. A simplification of habitat complexity is expected by potential shifts towards cup coral CWC communities, or towards octocoral coral gardens in canyons, as already observed in tropical shallow coral reefs due to global warming (Ruzicka et al., 2013; Rossi et al., 2017).

5. CHAPTER 5: General conclusions

5.1. Synopsis of the results

This section is dedicated to summarizing the main findings presented in the Chapters 2 to 4, based on the research questions proposed in section 1.5.1.

Q1 – What are the megabenthic communities found on walls of Blanes Canyon?

Chapter 2 of this thesis demonstrated that Blanes Canyon is an important CWC habitat in the Mediterranean Sea, including 13 CWC species, along with associated fauna composed of ascidian, sponges, crustaceans, and fish. The depth range explored (450 – 1200 m) showed that CWCs were present on canyon walls, where different types of hard substrate are present, and at depths that correspond to the LIW and WMDW. However, an along canyon gradient emerged based on different species occurring in distinct areas of the canyon. More specifically, colonial scleractinian corals (*D. pertusum* and *M. oculata*) were found mostly in the upper canyon head, closer to the coast. Further from the coast, within the canyon head and on the east canyon branch, prevailing coral species belonged to octocorals (*C. verticillata*, *A. hirsuta*, *M. lepida*) and black corals (*A. dichotoma*, *L. glaberrima*). The only species that was found across all sites and depths was *D. dianthus*. The upper canyon head is known to experience high energy events such as dense shelf water cascading or eastern storms which can be deleterious for other CWCs with erect growth forms such as *L. glaberrima*. On the other hand, the solid $CaCO_3$ skeleton of colonial scleractinians is more likely to sustain such violent events. On the east canyon branch hemipelagic sedimentation and advection of fine suspended particles transported along the margin by the Northern Current are proposed as main hydrodynamic and sediment transport mechanism. Different environmental conditions governing different parts of the canyon contribute to increased spatial heterogeneity, which is reflected in the benthic communities, and more specifically, in CWC communities.

Q2 – What are the water column characteristics that may affect CWCs in Blanes Canyon and how does bottom trawling modify them?

Chapter 3 of this thesis focused on the oceanographic conditions and composition of suspended particles during fishing closure in locations close to CWCs in Blanes Canyon, as well as on the characteristics of an enhanced BNL caused by trawling on a fishing ground along the canyon axis. The study showed that the upper canyon head has the potential to receive and retain fresh particulate matter exported from the surface, while more degraded particulate matter was found further from the coast, as in case of the east canyon branch, as well as in deeper parts of the canyon head. This discrepancy can be explained by the different dominating hydrodynamics in different parts of the canyon. More specifically, in the upper canyon head occasional high energy events are likely to efficiently deliver fresh food to deeper areas, while in the east canyon branch and further down the canyon, hemipelagic sedimentation is more prominent. Lastly, the results showed that trawling in the canyon axis caused an enhanced BNL with resuspension of degraded particulate matter from bottom sediments.

Q3 – What are the effects of increased SSC related to bottom trawling on CWCs living on the canyon walls of Blanes Canyon?

Chapter 4 took an experimental approach towards understanding the effects of increased SSC, mimicking trawl-induced turbidity currents, on CWC survival, growth, and physiology. The low concentration used was in line with low trawling intensity, as recorded in the Chapter 3, while high concentration can be found during intensive trawling activity (Martín et al., 2014c) or severe storm events (Sanchez-Vidal et al., 2012). This study constitutes the first long-term, multi-species study that compared octocoral, scleractinian and antipatharian species. The results showed species-specific responses of the studied CWCs after 9 months of exposure. Survival was the most prominent response, showcasing the high vulnerability of colonial scleractinian species (*D. pertusum* and *M. oculata*), as well as the black coral *L. glaberrima* to increased SSC. On the other hand, the cup coral *D. dianthus* and octocoral *M. lepida* showed no signs of distress after long-term exposure to increased SSC. Moreover, this study provided first long-term data on rarely studied species such as *L. glaberrima* and *M. lepida.* These species revealed lower metabolic rates compared to scleractinian corals, in line with previous studies (Larsson et al., 2013b; Maier et al., 2019c; Rakka et al., 2021).

5.2. Indirect impacts of trawling on CWCs of Blanes Canyon

The most frequently visited trawling grounds in Blanes Canyon are found in the vicinity of the canyon head (Fig. 1.2). As a result, this area is expected to receive more frequent events of high SSC, compared to other locations within the canyon (Ramirez-Llodra et al., 2010; Paradis et al., 2018; Soriano et al., 2020). According to Chapter 2, the canyon head was an important area for colonial scleractinians. Their presence in an environment of increased SSC contrasts with the findings from Chapter 4, that showed their high vulnerability to increased SSC. Food source and availability is proposed to explain this difference. The upper canyon head was shown to harbour fresh particulate matter (Chapter 3) with high amounts of nitrogen, possibly coming from surface production. As discussed in Chapter 4, fresh sources of nitrogen, like live zooplankton, have been identified as important for vital physiological processes of CWCs, such as growth and reproduction (Naumann et al., 2011, 2015; Rakka et al., 2021). This food source, which was not provided in the experiments performed in Chapter 4, might be essential to counteract the stress responses caused by high SSC. Nevertheless, scleractinian colonies that were found on canyon walls were usually found growing downwards, with clumps of sediment deposited over death coral frameworks (Fig. 2.9); which possibly suggests an evading mechanism due to increased sediment deposition (Chapter 2). This highlights that although these species can withstand the current high impact of SSC, there might actually be trade-offs for their growth and physiology. More specifically, as shown in Chapter 3, the increased trawling in the area delivers not only sediment, but also more degraded particulate matter, which may cause a dilution of the important fresh food sources. In the long-term, and in combination with high SSC, this might alter energy allocation with deleterious results for coral growth and reproduction. This, in combination with potential additional stressors driven by climate change, such as temperature rise and a decrease of available food (Levin and Le Bris, 2015; Sweetman et al., 2017) may hamper the ability of these important habitat forming species to cope with the indirect trawling effects that they are experiencing now, and are seemingly not affected by.

Comparatively to the canyon head, the east canyon branch receives fewer trawling resuspension effects. This area was identified as characterized by high densities of *L. glaberrima* and *M. lepida*. While *M. lepida* was also found spread among almost all studied sites in the canyon, *L. glaberrima* showed preference to more protected east canyon walls which are characterized by prevailing hemipelagic sedimentation instead of erosional processes, as those inferred for the west canyon wall. Morphological complexity and longevity of this species suggests a necessity for more stable conditions to thrive, especially in absence of major sediment transport events that could bring coarse sediments at high speeds (> 50 cm s^{-1}), such as those occurring at the canyon head during major storm events (Sanchez-Vidal et al., 2012). Chapter 4 showed that *L. glaberrima* is highly vulnerable to SSC, while *M. lepida* did not show signs of distress. Moreover, physiological measurements performed in Chapter 4, showed that these two species have lower metabolic rates, and therefore lower energy demands compared to scleractinian species. Previous studies have highlighted the ability of octocorals to prevail in areas with seasonal food input, where low metabolic rates are essential during periods with low food availability, while sporadical inputs of fresh food is used to replenish lipid reserves and reproductive cycles (Coma and Ribes, 2003; Rossi et al., 2006). This corroborates both the presence of *M. lepida* in the east canyon branch where relatively more degraded food was found (Chapter 3), as well as its relatively higher resilience to high SSC.

Among all the studied species, two species stood out in the Chapter 2 and 4, *D. dianthus* and *M. lepida*. Both were found spread in the canyon and showed no signs of stress in higher SSC. These findings demonstrate their resilience to various environmental conditions. Recently, studies have shown that *D. dianthus* is a flexible species that can acclimate to a range of different environmental conditions, by increasing its metabolism, investing into higher growth rates or lipid reserves in favourable conditions, and decreasing its metabolism, including growth rate and respiration, under unfavourable conditions (Höfer et al., 2018; Maier et al., 2021). The latter was also observed in the Chapter 4 of this thesis. This metabolic plasticity may be the reason why this species has a wide depth and geographic range (Addamo, 2019; Beck et al., 2022). Moreover, in Chapter 2, its ecological role as a foundation species was discussed, because in many sites studied in Blanes Canyon, *D. dianthus* served as a biogenic substrate upon which other CWCs settled on. One of them was *M. lepida*, which was studied in an experimental setting for the first time in this thesis, providing valuable information on the species. Potential reasons why *M. lepida* can thrive in various settings in Blanes Canyon include low energetic demands which make it suitable to survive in areas of limited food supply.

Moreover, its relatively small size (compared to *L. glaberrima*) and flexibility of the organic skeleton provide means to avoid sediment settlement on the polyps without needing to spend energy on mucus production for cleaning, as in the case of colonial scleractinians that do not have that flexibility (Allers et al., 2013; Larsson et al., 2013b). Although both *D. dianthus* and *M. lepida* seemed to be widespread species not affected by high SSC, it is not known whether long-term impacts may affect them, especially under combined impacts of trawling and climate change.

5.3. Future research

Research on submarine canyon communities and trawling effects should be continued as more understanding of these dynamic environments is needed to guide marine spatial management and conservation goals under global change. More specifically, exploration of shallower areas in Blanes Canyon and deeper areas in other submarine canyons of the Catalan margin and Gulf of Lions could fill in the knowledge gaps identified in this thesis. This would facilitate comparisons between different environments and would help to understand better the indirect impacts of bottom trawling. High resolution studies of submarine canyons, such those presented in this thesis, are encouraged since they can help understand the drivers of spatial heterogeneity as well as the consequences they bear for different species. Additionally, the temporal variability of environmental conditions should be included, as it shapes species distribution. Daily variations have shown to be important in CWC habitats, this should be considered for Blanes Canyon as well. Additionally, food related studies such as bentho-pelagic coupling, zooplankton vertical migrations and a trophic analysis would be beneficial. This is extremely important in the framework of climate change, as some events may change in frequency and/or intensity in the future. The indirect impacts of trawling on canyon communities should be investigated in more detail, especially with *in situ* observations. Trawling impacts, both as increased SSC and alteration of environmental conditions, can have more long-lasting effects on energy allocation and reproduction of CWCs, as well as on larval survival and dispersal, all of which have important repercussions for species survival. Finally, more studies should include cold-water octocoral and black coral species, as our understanding of their physiology is still limited (Rossi et al., 2006; DeLeo et al., 2016; Rakka et al., 2021). New techniques, such as the photogrammetry approach demonstrated in this thesis, can provide insight into their biology and ecology with high precision.

5.4. Concluding remarks

This thesis is based on a multidisciplinary approach towards assessment of indirect impacts of bottom trawling on CWCs living on walls of Blanes Canyon. The study provided:

- a detailed description of CWC species found in Blanes Canyon,
- a detailed characterization of the natural oceanographic conditions and suspended particles composition surrounding CWCs, without interference of bottom trawling,
- a detailed insight to the indirect impacts of trawling, by describing an enhanced bottom nepheloid layer formed directly after a trawl event,
- an experimental, physiological perspective on the effects of increased SSC on six Mediterranean CWCs.

The thesis demonstrated that trawling could have negative, indirect impacts on important habitat forming CWCs. These impacts are species-specific, showing that long-term trawling may affect the composition of future CWC communities in Blanes Canyon.

Further studies are therefore essential to understand the combined impacts of trawling and other anthropogenic disturbances.

6. Supplementary materials

6.1. Appendix A: Supplementary materials of Chapter 2

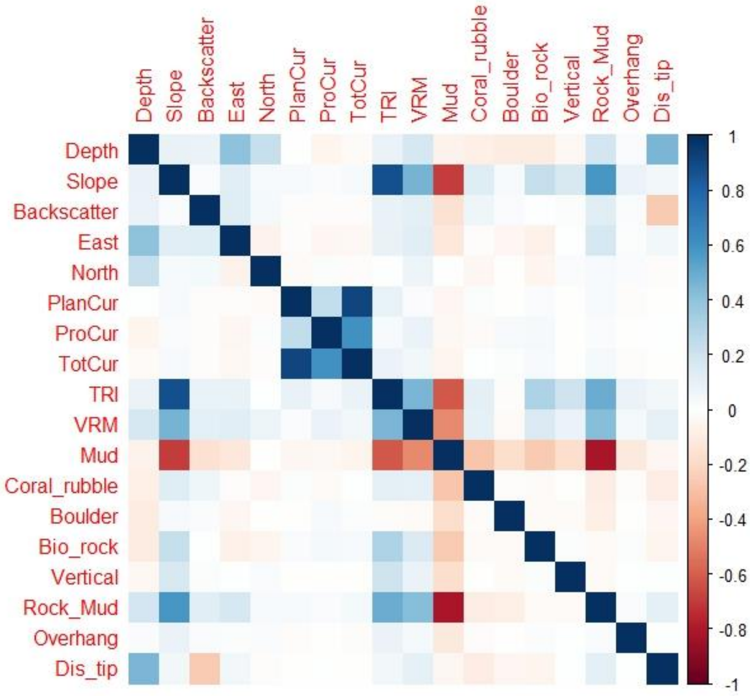
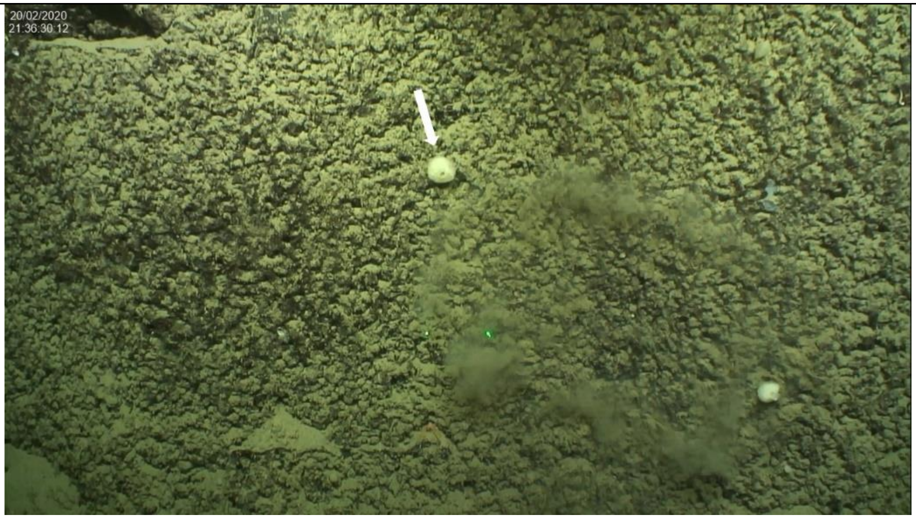
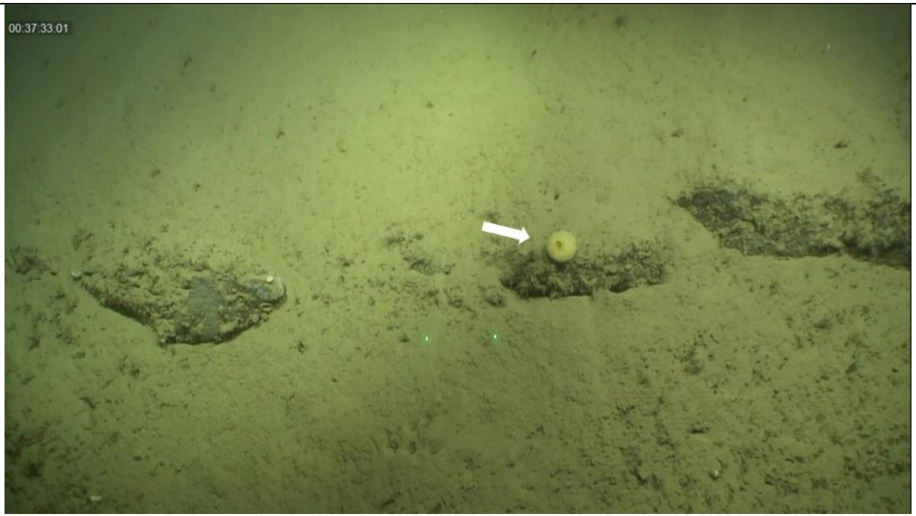
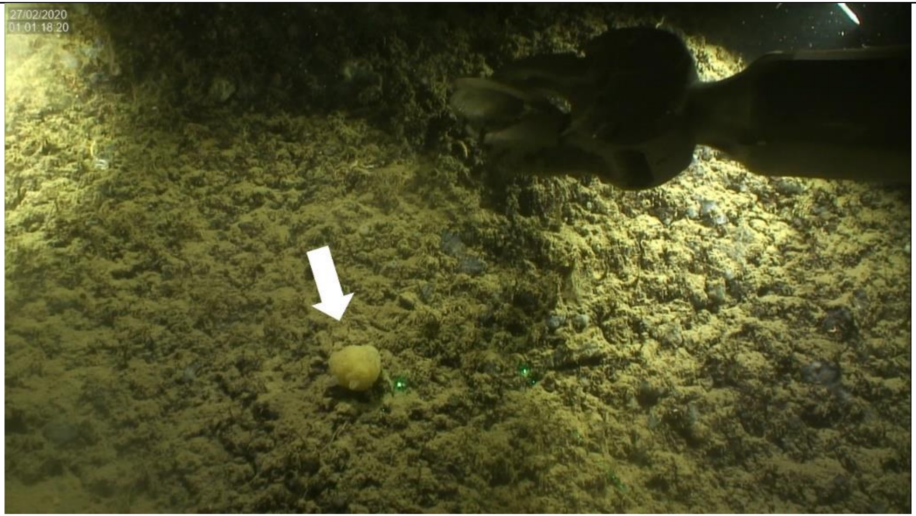
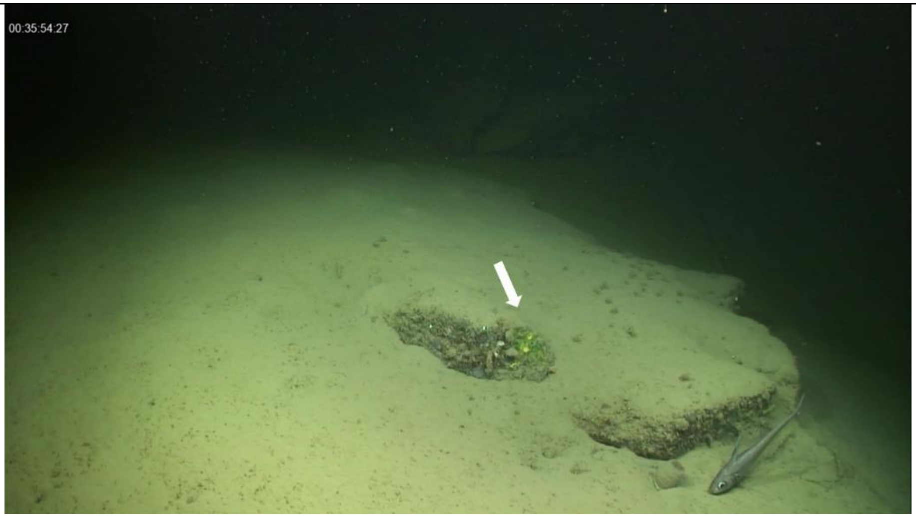


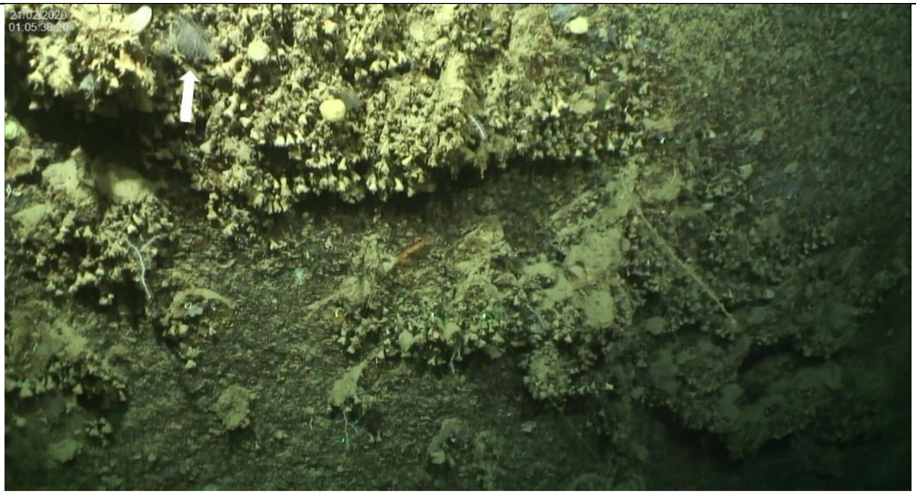
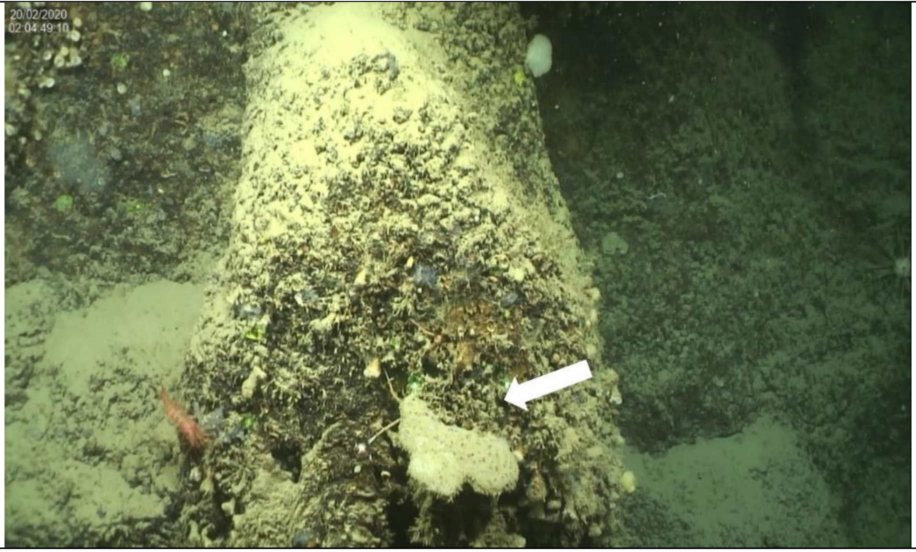
Figure 6.1. Correlation matrix of environmental variables

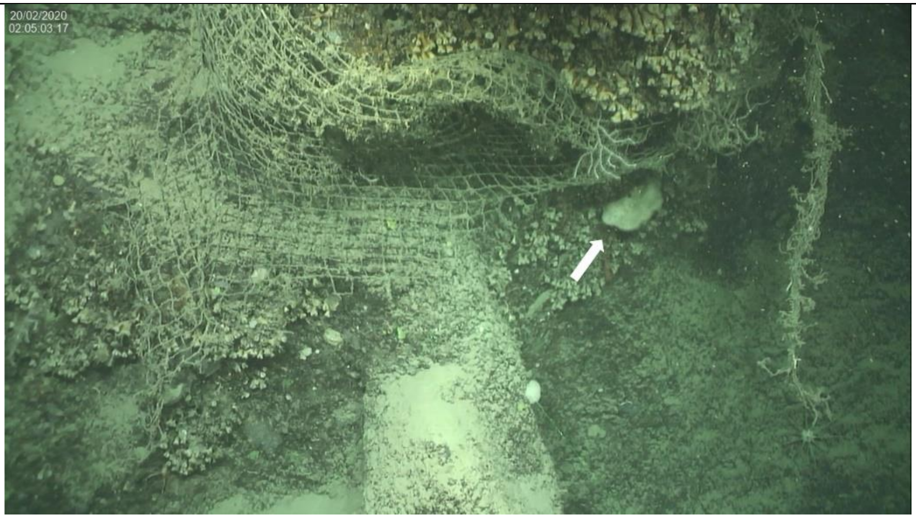
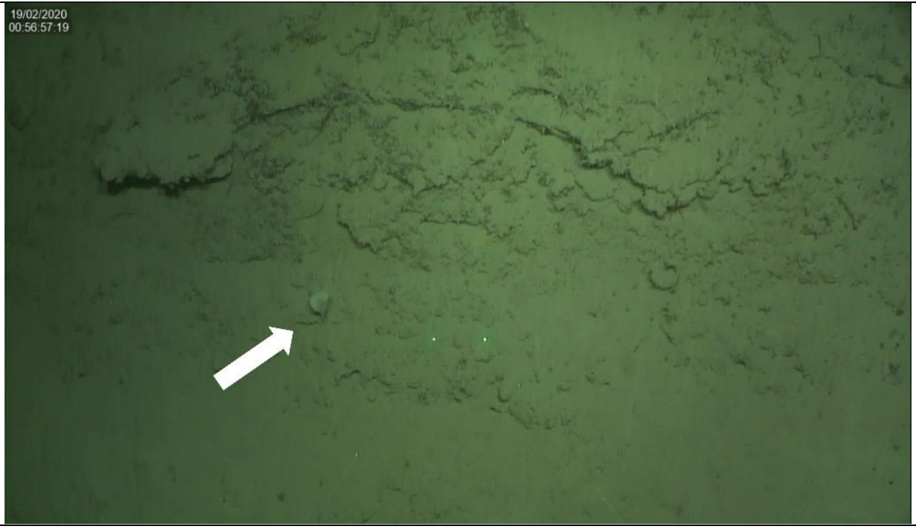
Table 6.1. Species identification guide for Blanes Canyon

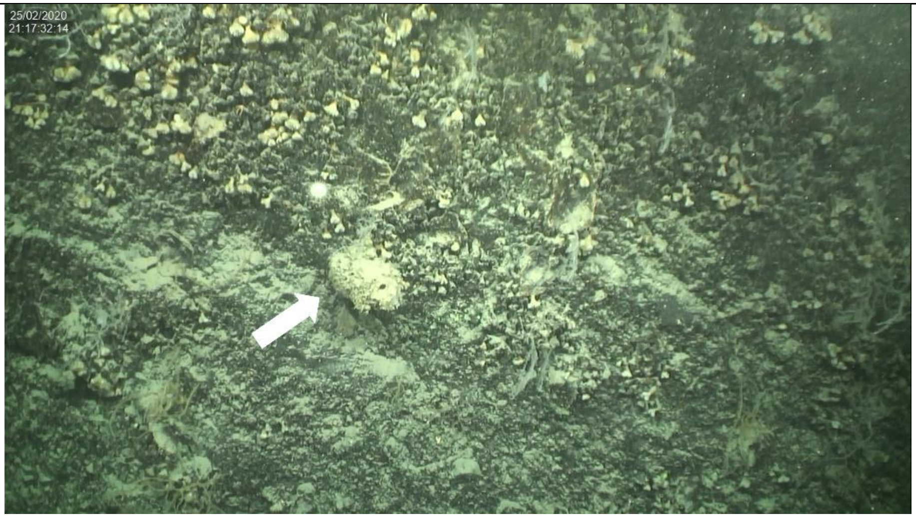
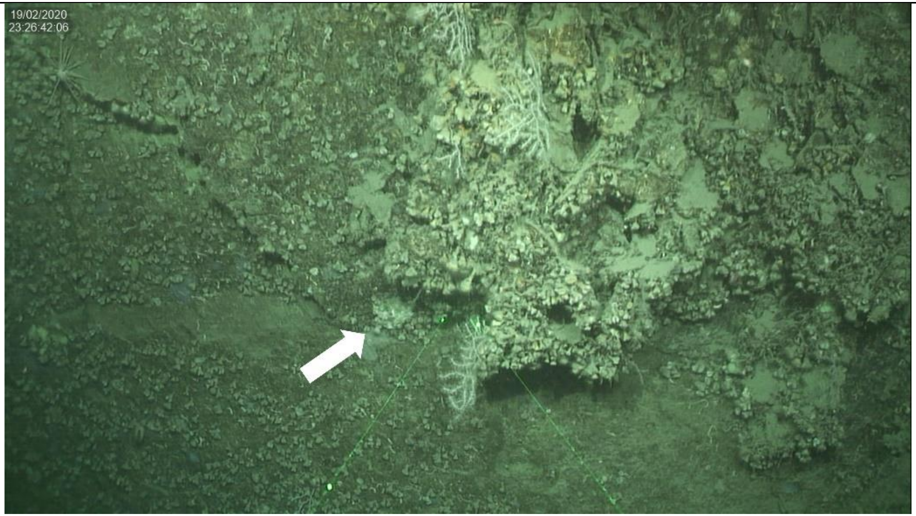
Morphospecies details	**Morphospecies *in situ* photo**	**Transect number where the morphospecies was found:**
Phylum: Porifera Class: Demospongiae Family: Polymastiidae AphiaID: 134243 *Atergia corticata* Stephens, 1915		6, 15, 18, 26, 27, 28, 30, 31, 33, 34, 35, 37, 43, 44, 47, 49, 50, 52

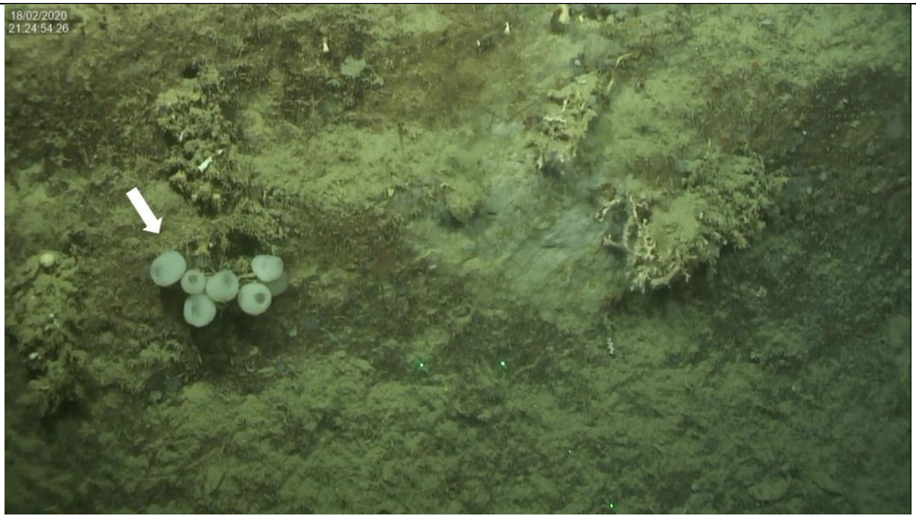
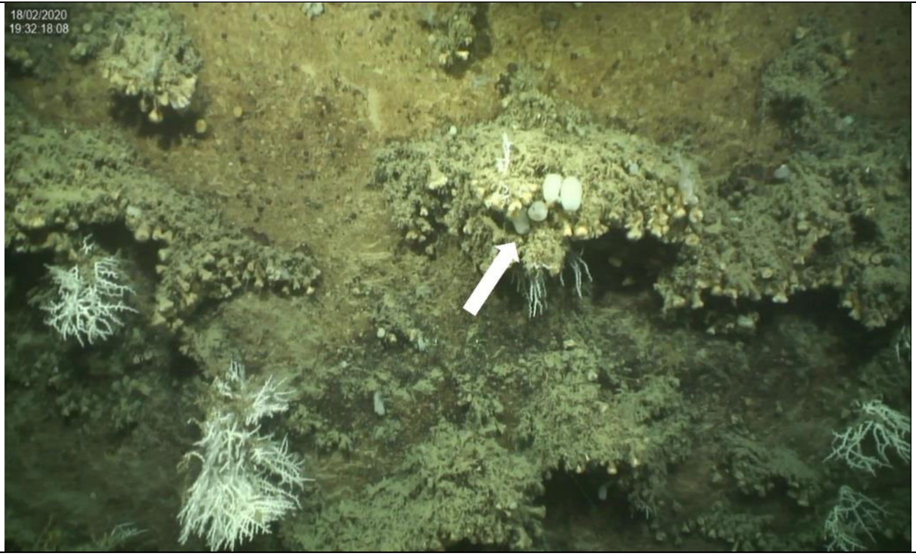
Phylum: Porifera Class: Demospongiae Family: Suberitidae AphiaID: 134275 *Suberites carnosus* (Johnston, 1842)		9, 10, 12, 13, 14, 15, 16, 17, 18, 34, 35, 36, 37, 38, 40, 42, 44, 45, 46, 47, 48, 49, 50, 52, 54, 55
Phylum: Porifera Class: Demospongiae Family: Polymastiidae AphiaID: 132046 *Polymastia* sp.1 Bowerbank, 1862		10, 12, 15, 16, 17, 37, 40, 43, 55

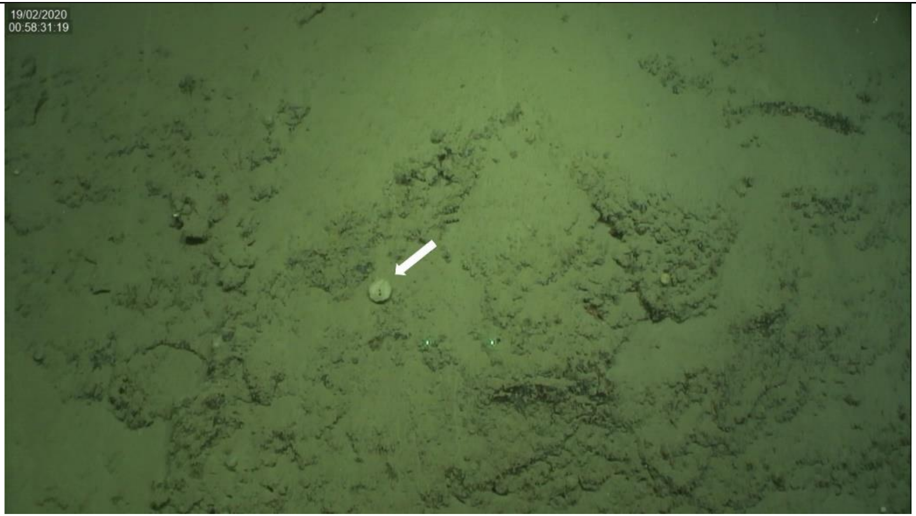
Phylum: Porifera Class: Demospongiae Family: Ianthellidae AphiaID: 169682 *Hexadella dedritifera* Topsent, 1913		3, 6, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 30, 31, 33, 34, 35, 38, 40, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 53, 54, 56
Phylum: Porifera Class: Demospongiae Familiy: Hamacanthidae AphiaID: 168431 *Hamacantha (Vomerula) falcula (*Bowerbank, 1874)		2, 4, 6, 7, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 30, 31, 33, 34, 35, 36, 37, 38, 39, 41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 53, 54, 55, 56

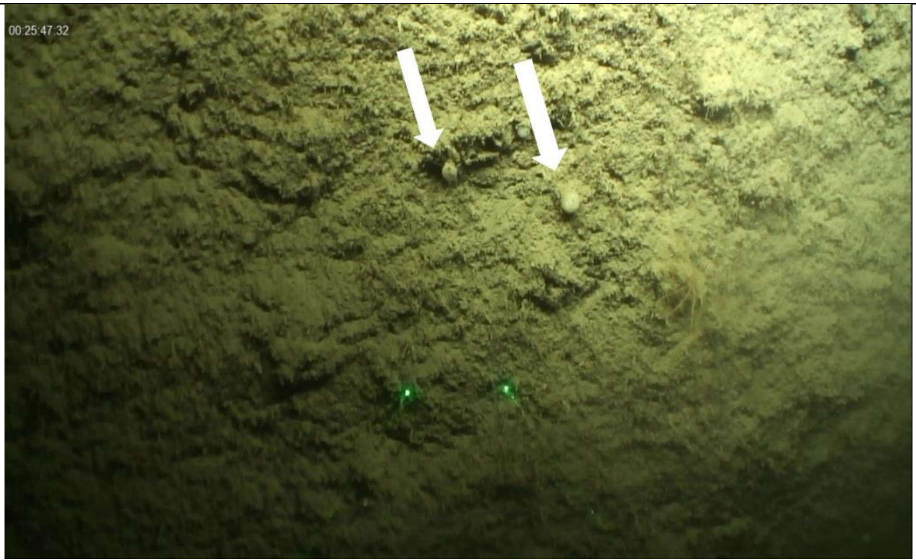
Phylum: Porifera Class: Demospongiae Familiy: Cladorhizidae AphiaID: 133188 *Cladorhiza abyssicola* Sars, 1872		34, 42, 50, 55
Phylum: Porifera Class: Demospongiae Familiy: Vulcanellidae AphiaID: 134083 *Poecillastra compressa* (Bowerbank, 1866)		12, 15, 17, 24, 34, 35, 40, 44, 48, 49, 51, 52, 53, 55

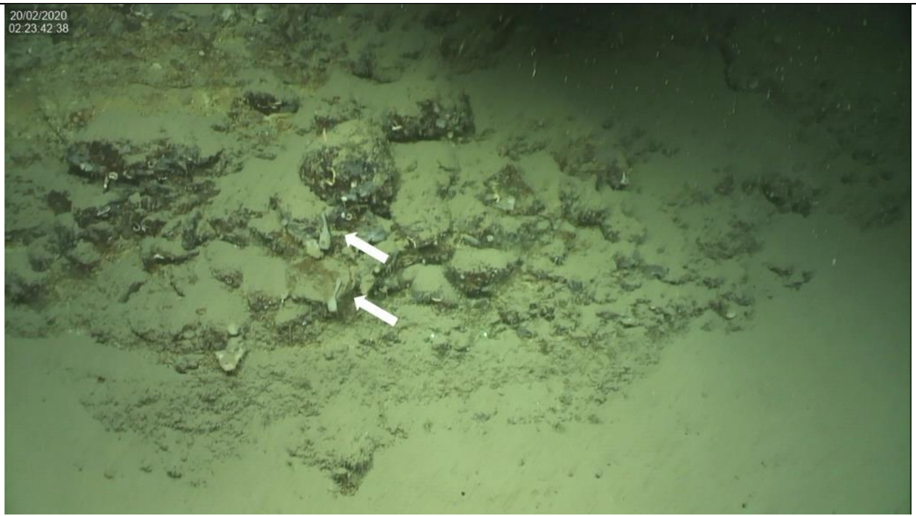
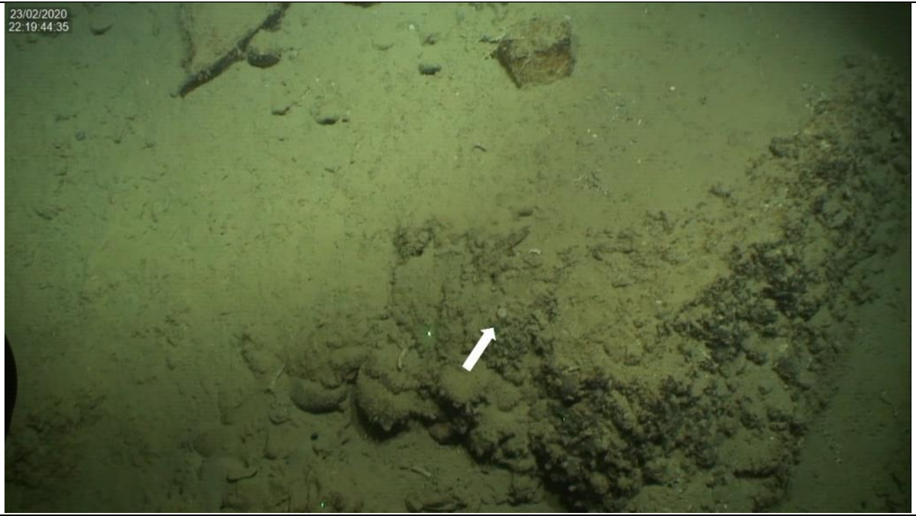
Phylum: Porifera Class: Demospongiae Familiy: Pachastrellidae AphiaID: 134078 *Pachastrella monilifera* Schmidt, 1868		11, 12, 16, 17, 18, 30, 33, 34, 36, 37, 38, 43, 44, 45, 46, 47, 48, 49, 50, 52, 53
Phylum: Porifera Class: Demospongiae Familiy: Bubaridae AphiaID: 132509 *Phakellia robusta* Bowerbank, 1866		15, 18, 26, 31, 33, 37, 40, 41, 43, 44, 45, 46, 47, 49, 50, 52

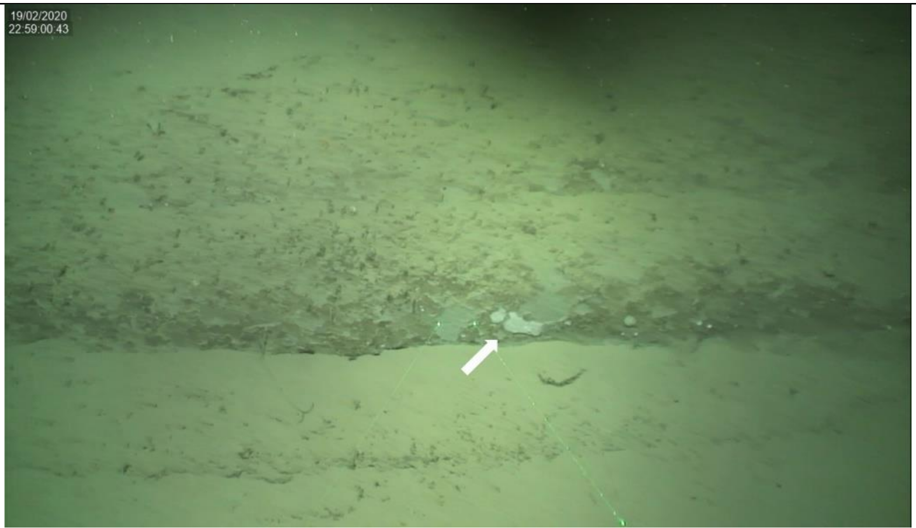
Phylum: Porifera Class: Demospongiae AphiaID: 131602 Astrophorina sp.1		18, 30, 49
Phylum: Porifera Class: Demospongiae AphiaID: 131602 Astrophorina sp.1		9, 33, 37, 48

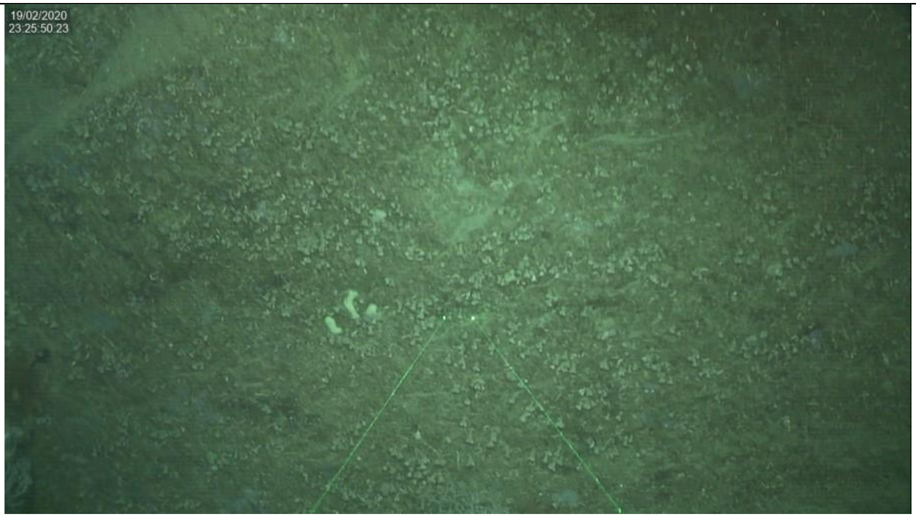
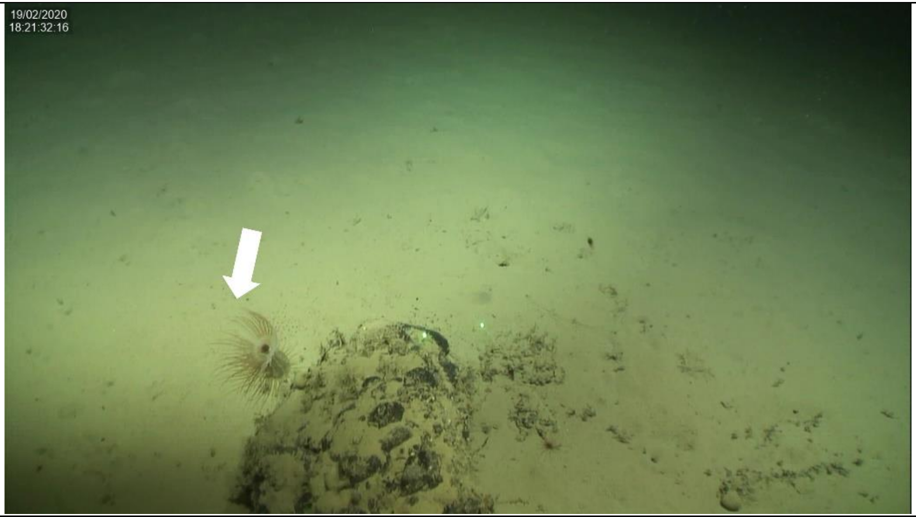
Phylum: Porifera Class: Hexactinellida Familiy: Rossellidae AphiaID: 829372 *Sympagella delauzei* Boury-Esnault, Vacelet, Reiswig & Chevaldonn, 2015		6, 9, 10, 12
Phylum: Porifera Class: Hexactinellida Familiy: Leucopsacidae AphiaID: 134408 *Oopsacas minuta* Topsent, 1927		3, 4, 5, 6, 9, 10, 12, 13, 16, 50

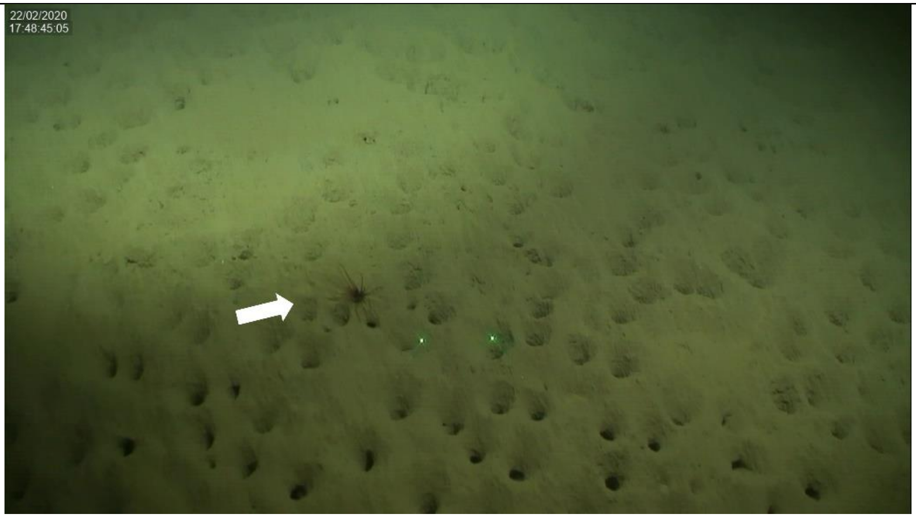
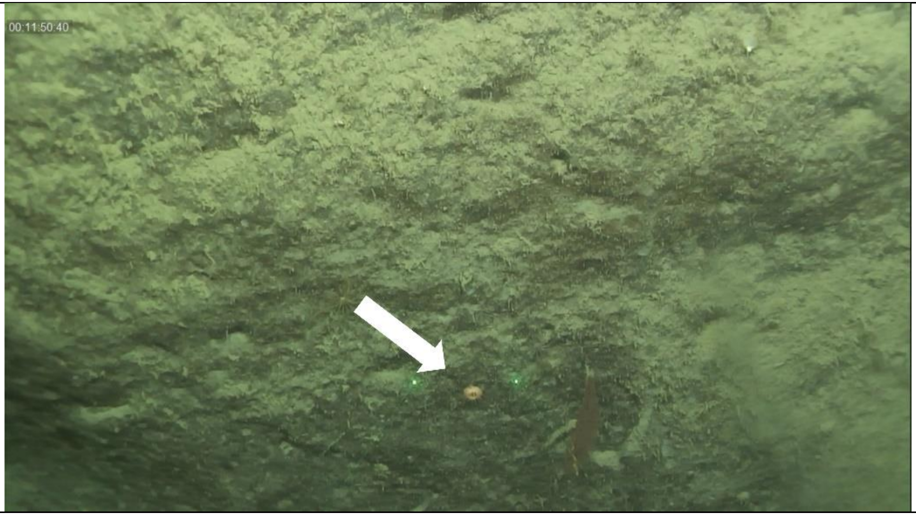
Phylum: Porifera Class: Hexactinellida Familiy: Tretodictyidae AphiaID: 956229 *Tretodictyum reiswigi* Boury-Esnault, Vacelet & Chevaldonn, 2017		9, 10, 15, 17, 18, 30, 31, 33, 34, 35, 39, 43, 44, 49, 52, 55
Phylum: Porifera AphiaID: 558 Porifera sp.2		12, 24, 28, 43, 45, 47, 50, 52

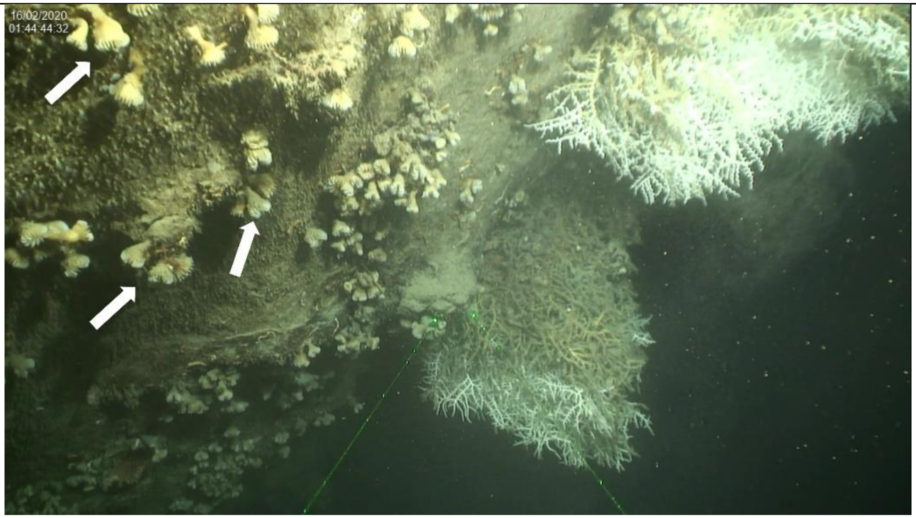
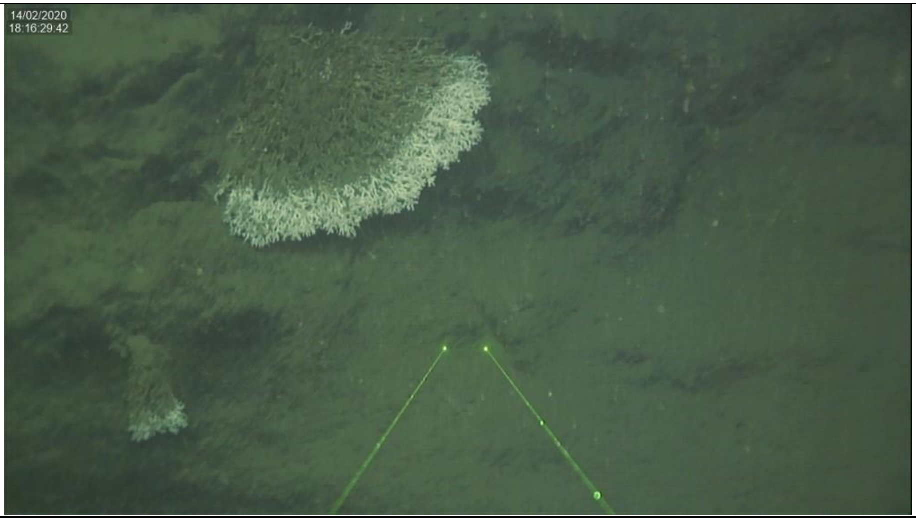
Phylum: Porifera AphiaID: 558 Porifera sp.3		2, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 22, 23, 26, 27, 28, 29, 30, 31, 33, 34, 35, 36, 37, 38, 39, 40, 41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 53, 54, 55, 56
Phylum: Porifera AphiaID: 558 Porifera sp.4		2, 6, 8, 10, 12, 14, 15, 17, 21, 26, 27, 28, 31, 33, 36, 41, 44, 45, 46, 48, 54, 56

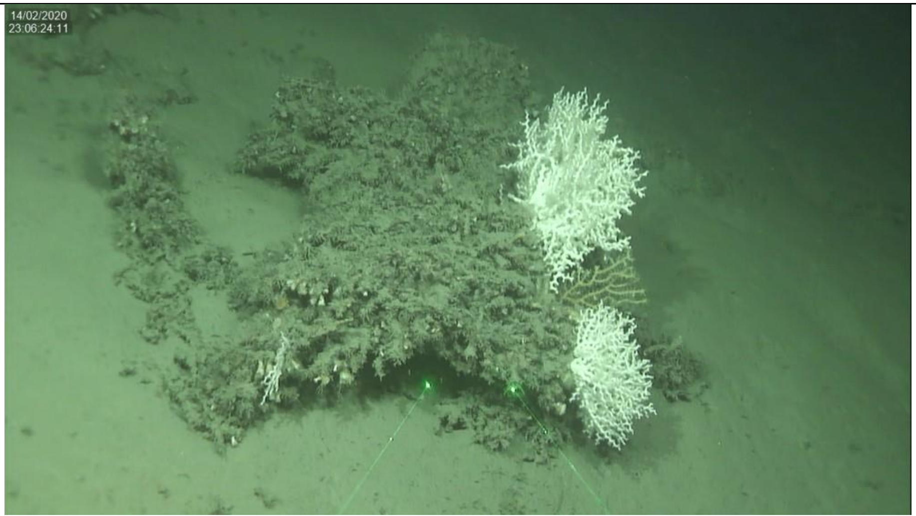
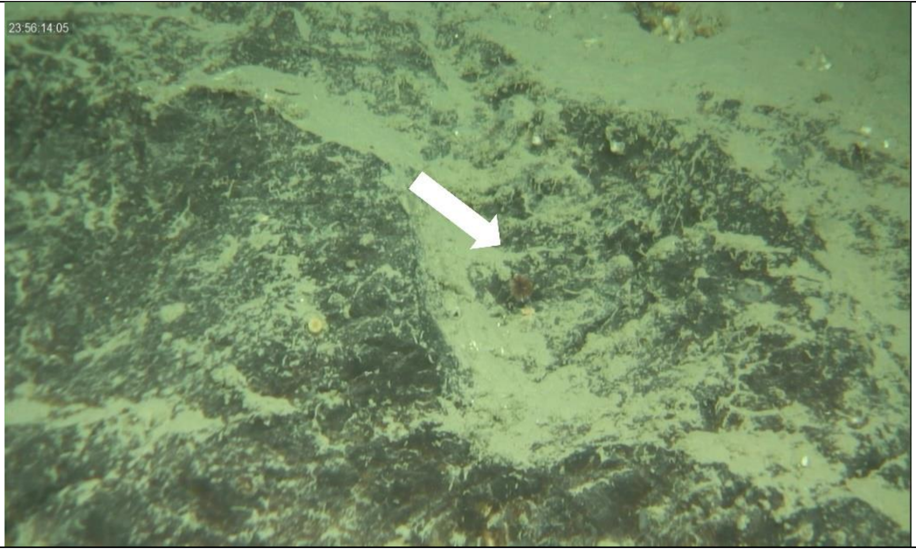
Phylum: Porifera AphiaID: 558 Porifera sp.5		17, 49
Phylum: Porifera AphiaID: 558 Porifera sp.6		7, 8, 9, 10, 11, 13, 14, 15, 16, 17, 18, 30, 31, 33, 34, 35, 37, 38, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 53, 54, 55

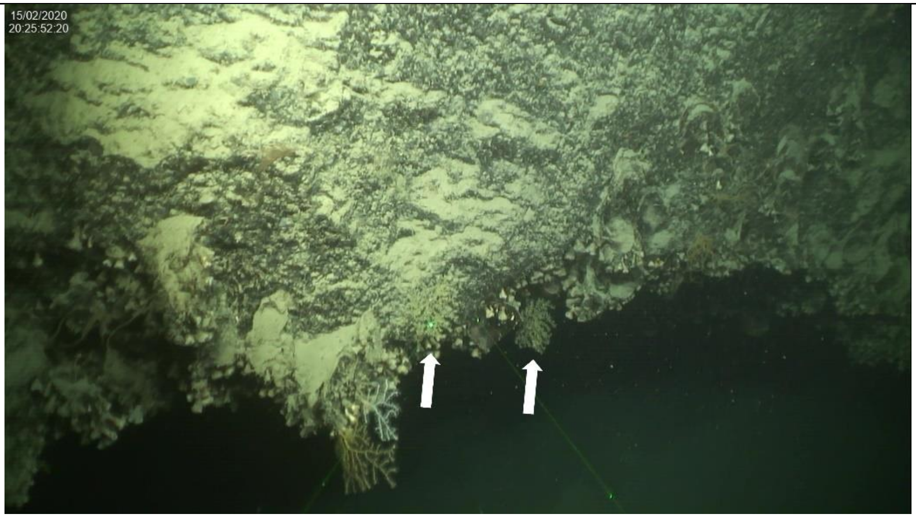
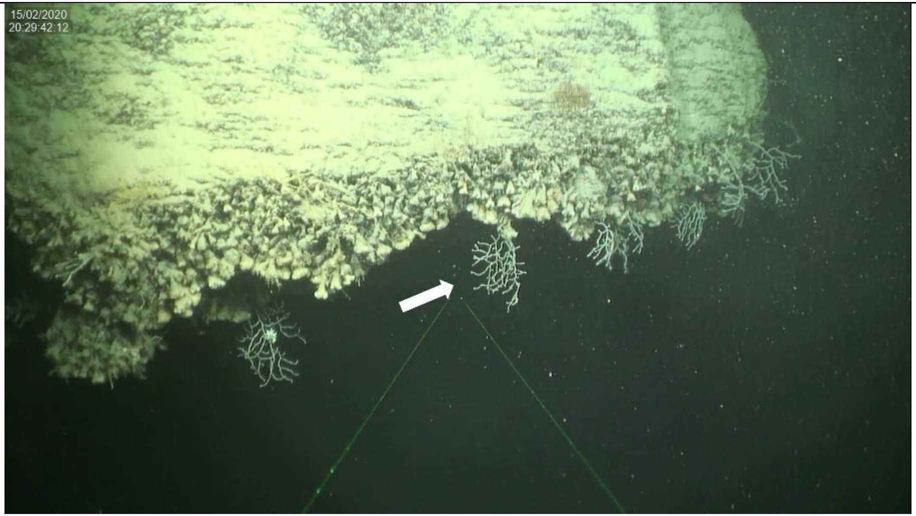
Phylum: Porifera AphiaID: 558 Encrusting porifera sp.1		10, 25, 27, 43, 44, 48, 53
Phylum: Porifera AphiaID: 558 Encrusting porifera sp.2		10, 12, 13, 15, 17, 35, 44

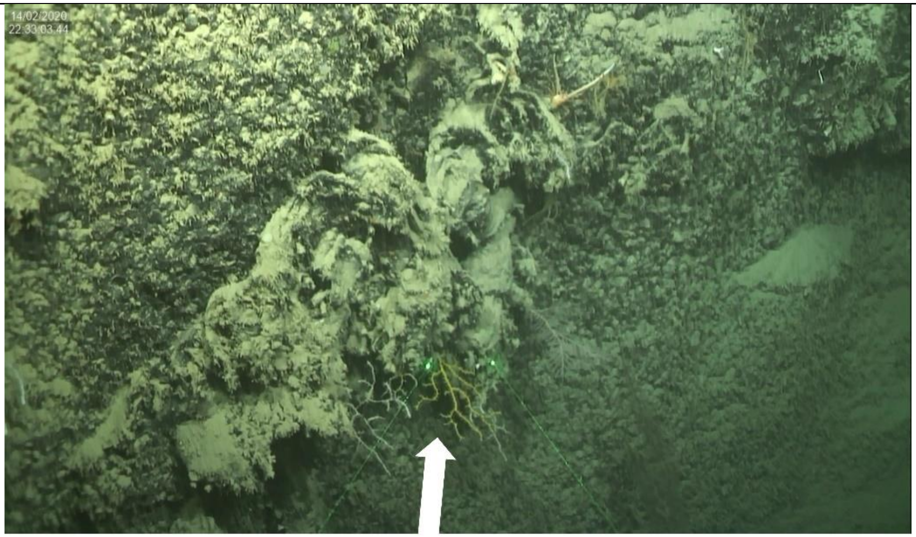
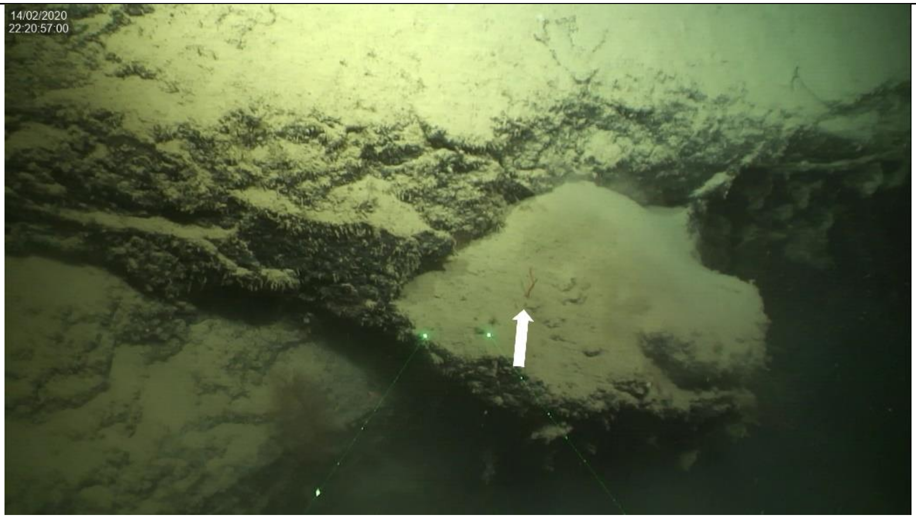
Phylum: Porifera AphiaID: 558 Encrusting porifera sp.3		48
Phylum: Cnidaria Class: Anthozoa Familiy: Cerianthidae AphiaID: 100782 *Cerianthus* Delle Chiaje, 1841		1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 15, 16, 18, 19, 21, 22, 23, 24, 27, 28, 30, 31, 34, 35, 36, 37, 39, 40, 41, 43, 44, 46, 47, 48, 50, 51, 52, 53, 55, 56

Phylum: Cnidaria Class: Anthozoa Familiy: Arachnactidae AphiaID: 100779 *Arachnanthus* Carlgren, 1912		2, 4, 9, 16, 17, 18, 19, 21, 22, 23, 24, 28, 30, 33, 34, 35, 36, 39, 40, 41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 53, 55, 56
Phylum: Cnidaria Class: Anthozoa AphiaID: 1360 Actiniaria		6, 11, 13, 14, 15, 18, 28, 30, 31, 33, 34, 35, 43, 45, 46, 47, 49, 55

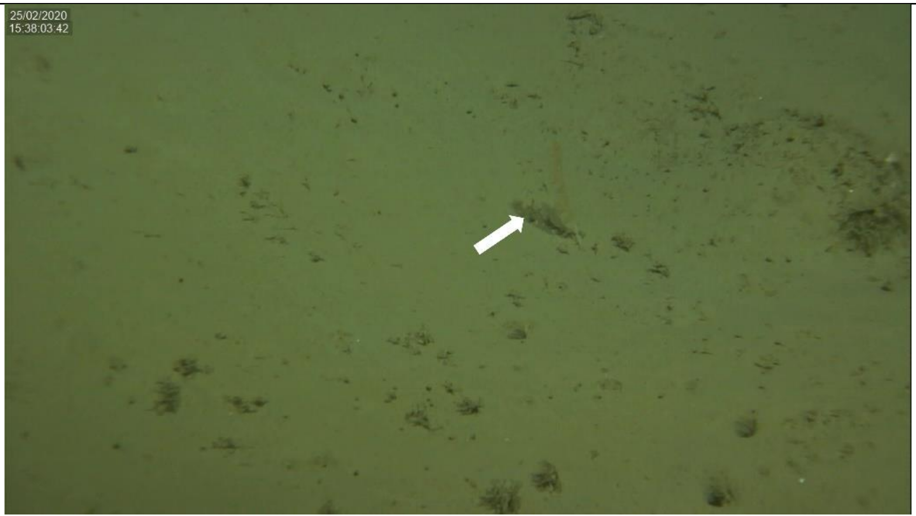
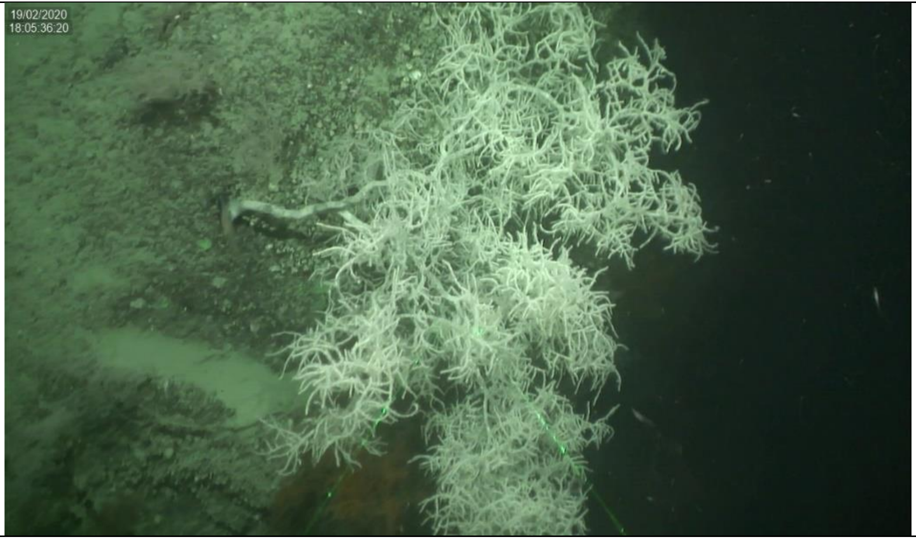
Phylum: Cnidaria Class: Anthozoa Familiy: Caryophylliidae AphiaID: 135159 *Desmophyllum dianthus* (Esper, 1794)		1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 37, 38, 39, 40, 41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 53, 54, 55, 56
Phylum: Cnidaria Class: Anthozoa Familiy: Caryophylliidae AphiaID: 1245747 *Desmophyllum pertusum* (Linnaeus, 1758)		1, 2, 3, 5, 6, 7, 8, 9, 10, 11, 12, 13, 19, 20, 21, 22, 23, 30, 31, 32

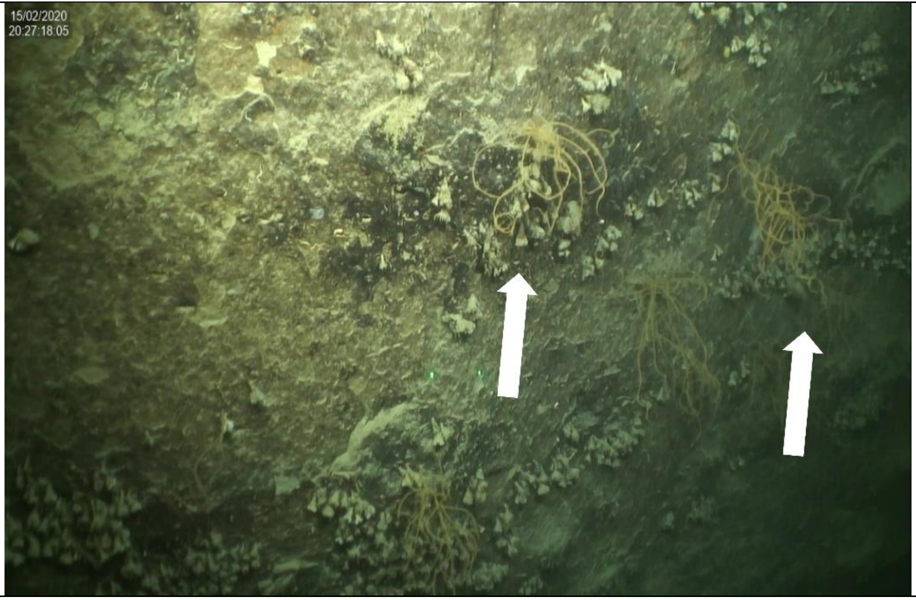
Phylum: Cnidaria Class: Anthozoa Familiy: Oculinidae AphiaID: 135209 *Madrepora oculata* Linnaeus, 1758		2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 15, 16, 17, 23, 24, 27, 28, 29, 31, 32, 34, 35, 38
Phylum: Cnidaria Class: Anthozoa Familiy: Flabellidae AphiaID: 135198 *Javania cailleti* (Duchassaing & Michelotti, 1864)		2, 7, 9, 30, 31, 33, 47, 56

Phylum: Cnidaria Class: Anthozoa Familiy: Paramuriceidae AphiaID: 125349 *Acanthogorgia hirsuta* Gray, 1857		23, 26, 28, 30, 31, 33
Phylum: Cnidaria Class: Anthozoa Familiy: Paramuriceidae AphiaID: 125383 *Muriceides lepida* Carpine & Grasshoff, 1975		3, 4, 5, 7, 9, 10, 14, 15, 18, 19, 23, 24, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 37, 38, 39, 40, 41, 42, 44, 45, 46, 47, 48, 49, 50, 51, 54, 55, 56

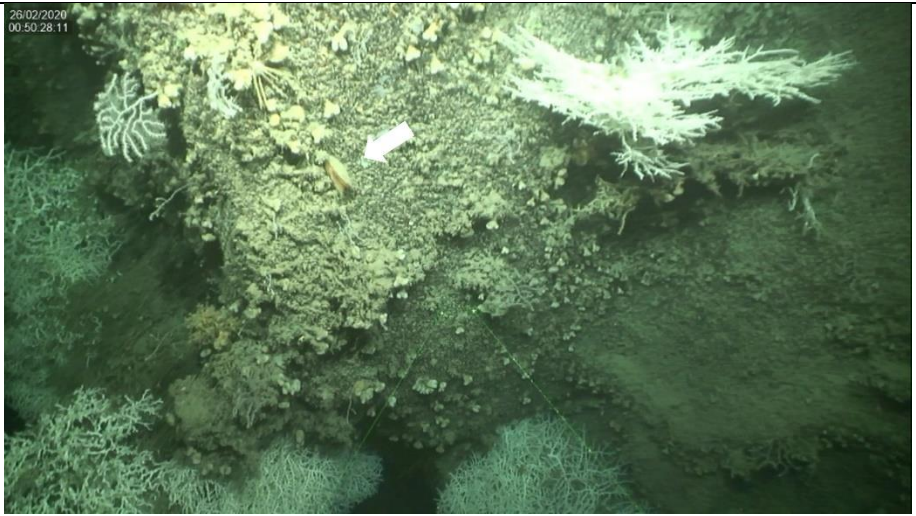
Phylum: Cnidaria Class: Anthozoa Familiy: Paramuriceidae AphiaID: 125392 *Placogorgia coronata* Carpine & Grasshoff, 1975		19, 23, 26, 30, 31
Phylum: Cnidaria Class: Anthozoa Familiy: Plexauridae AphiaID: 125400 *Swiftia dubia* (Thomson, 1929)		2, 6, 8, 9, 18, 19, 21, 22, 23, 26, 28, 30, 39, 47

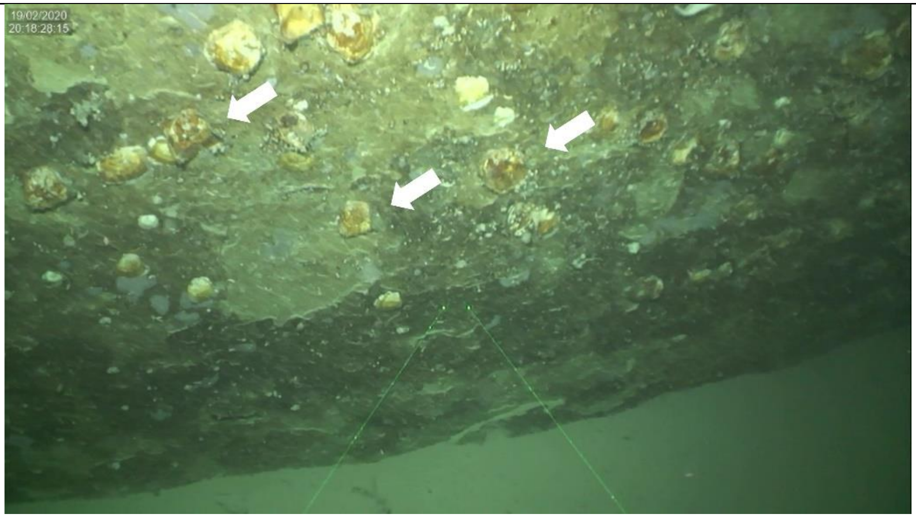
Phylum: Cnidaria Class: Anthozoa Familiy: Primnoidae AphiaID: 125405 *Callogorgia verticillata* (Pallas, 1766)		19, 21, 22, 23, 30, 31, 33
Phylum: Cnidaria Class: Anthozoa Familiy: Protoptilidae AphiaID: 128525 *Protoptilum carpenterii* Kölliker, 1872		50

Phylum: Cnidaria Class: Anthozoa Familiy: Keratoisididae AphiaID: 125373 *Isidella elongata* (Esper, 1788)		20
Phylum: Cnidaria Class: Anthozoa Familiy: Leiopathidae AphiaID: 103326 *Leiopathes glaberrima* (Esper, 1792)		34, 35, 36, 38, 39, 41, 44, 48, 50, 53, 54, 55

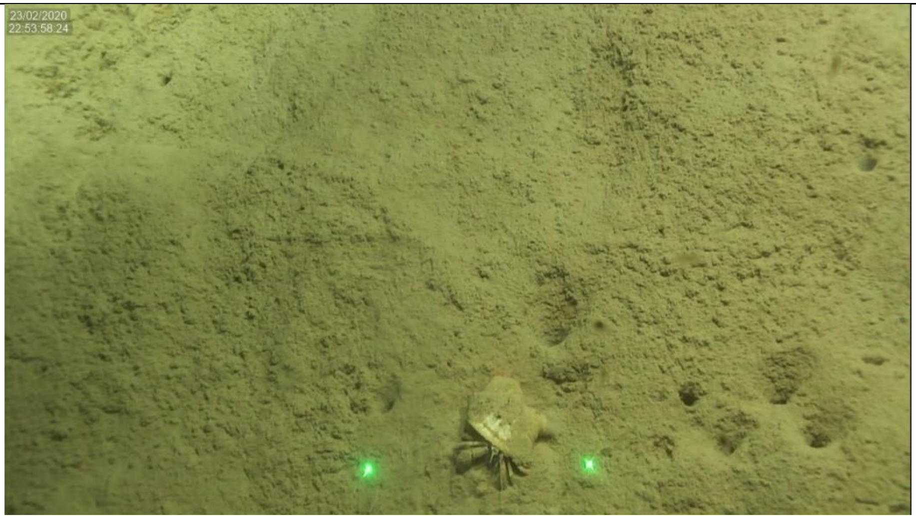
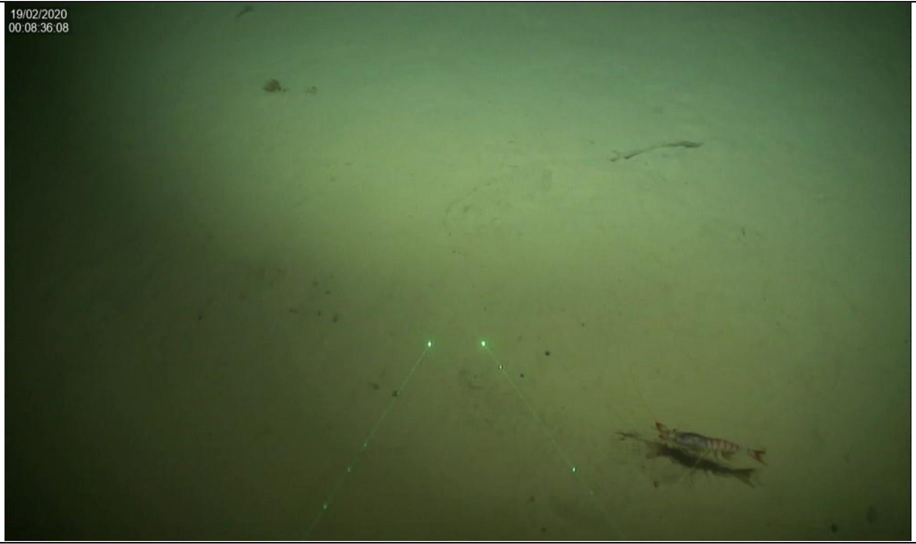
Phylum: Cnidaria Class: Anthozoa Familiy: Schizopathidae AphiaID: 283954 *Parantipathes* cf. *tetrasticha* (Pourtal, 1868)		2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 17, 18, 19, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 37, 38, 39, 42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 53, 54, 55, 56
Phylum: Cnidaria Class: Anthozoa Familiy: Antipathidae AphiaID: 103309 *Antipathes dichotoma* Pallas, 1766		3, 4, 9, 10, 19, 21, 22, 23, 26, 27, 28, 30, 31, 33, 34, 56

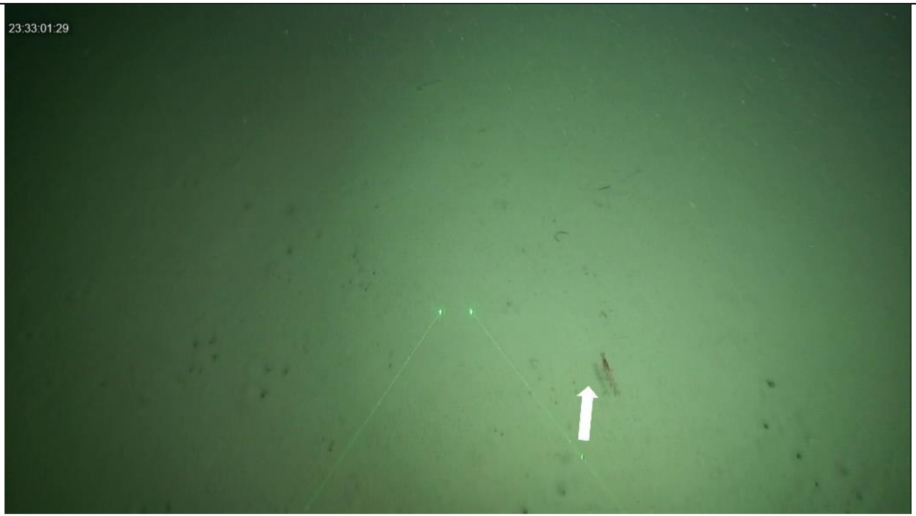
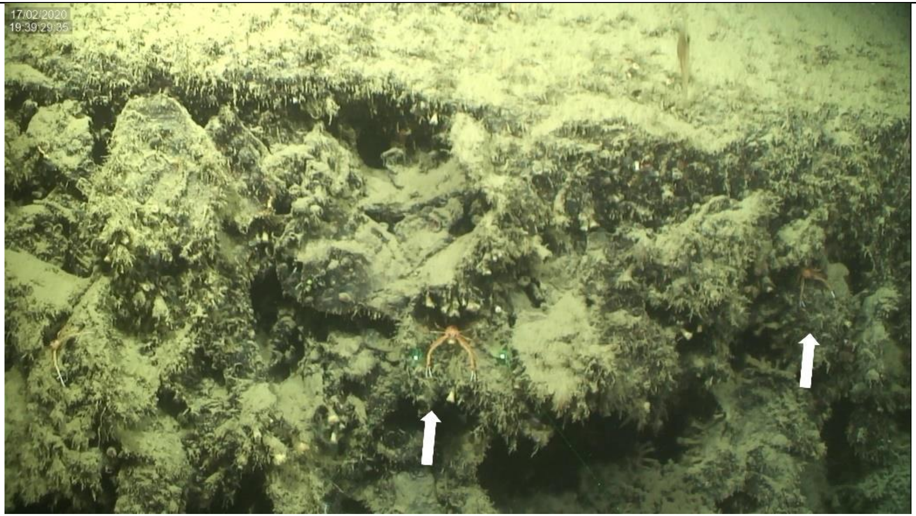
Phylum: Cnidaria Class: Anthozoa Familiy: Parazoanthidae AphiaID: 715090 cf. *Zibrowius* Sinniger, Ocaña & Baco, 2013		1
Phylum: Cnidaria Class: Anthozoa Familiy: Epizoanthidae AphiaID: 100790 cf. *Epizoanthus* Gray, 1867		22, 31, 40, 44, 48, 50, 52, 54

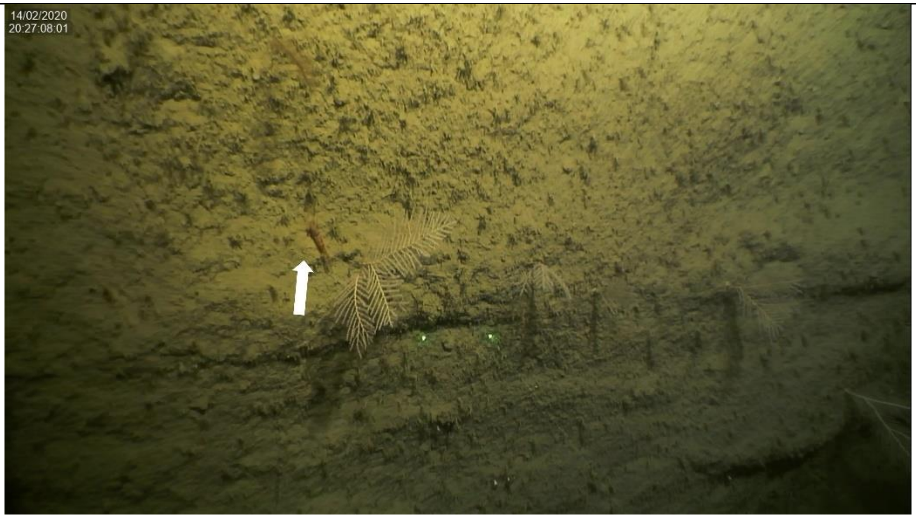
Phylum: Cnidaria Class: Scyphozoa Familiy: Periphyllidae AphiaID: 135294 *Periphylla periphylla* (Paron & Lesueur, 1810)		2, 13, 14, 16, 17, 18, 19, 27, 28, 29, 30, 31, 33, 51, 55
Phylum: Mollusca Class: Bivalvia Familiy: Limidae AphiaID: 140232 *Acesta excavata* (J. C. Fabricius, 1779)		26, 29, 30, 31, 34, 48

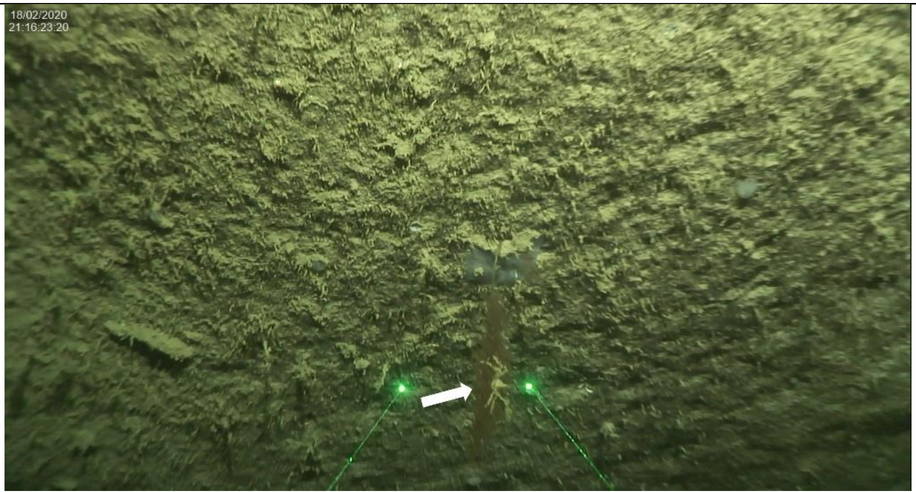
Phylum: Mollusca Class: Bivalvia Familiy: Gryphaeidae AphiaID: 379789 *Neopycnodonte zibrowii* Gofas, C. Salas & Taviani, 2009	 19/02/2020 20:18:28:15	2, 3, 5, 8, 10, 12, 15, 17, 25, 26, 31, 34, 35, 36, 37, 39, 44, 45, 46, 48, 49, 50, 51, 52
Phylum: Mollusca Class: Gastropoda AphiaID: 101	 22:38:51:14	1, 5, 8, 9, 10, 11, 19, 31, 33, 35, 37, 39, 40, 44, 45, 47, 48, 49, 50, 51, 52, 53, 55

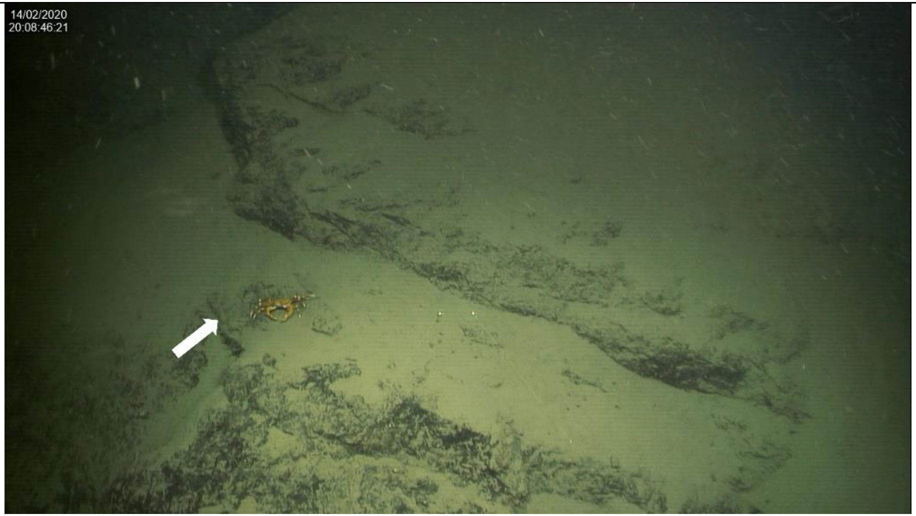
Phylum: Mollusca Class: Cephalopoda Familiy: Loliginidae AphiaID: 140271 *Loligo vulgaris* Lamarck, 1798		3, 38, 41
Phylum: Mollusca Class: Cephalopoda Familiy: Ommastrephidae AphiaID: 140621 cf. *Illex coindetii* (Vérany, 1839)		5

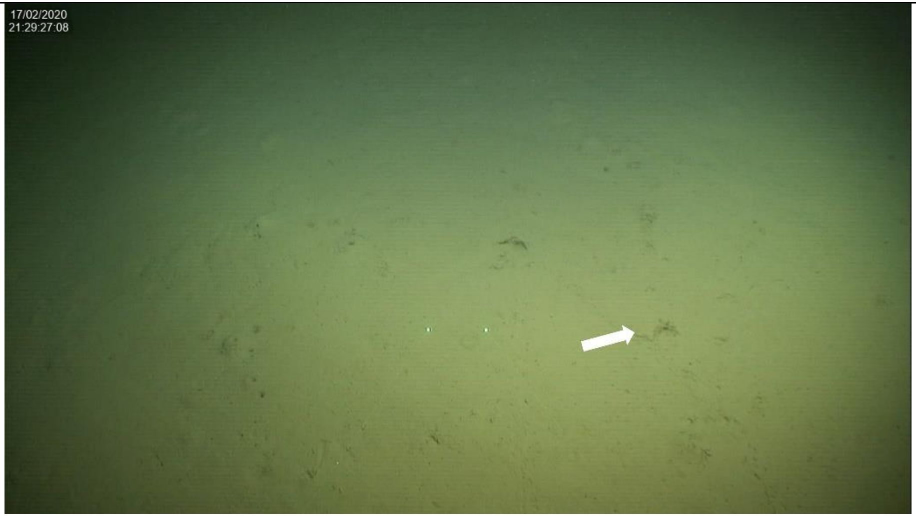
Phylum: Arthropoda Class: Malacostraca AphiaID: 106687 Hermit crab		3, 4, 7, 10, 11, 13, 15, 16, 18, 19, 21, 23, 24, 26, 27, 29, 30, 33, 34, 39, 42, 43, 44, 46, 47, 48, 49, 50, 51, 52, 56
Phylum: Arthropoda Class: Malacostraca Familiy: Aristeidae AphiaID: 107083 *Aristeus antennatus* (Risso, 1816)		9, 11, 12, 13, 16, 17, 18, 19, 21, 22, 23, 26, 27, 28, 30, 31, 33, 34, 35, 41, 42, 43, 45, 47, 50, 51, 53, 56

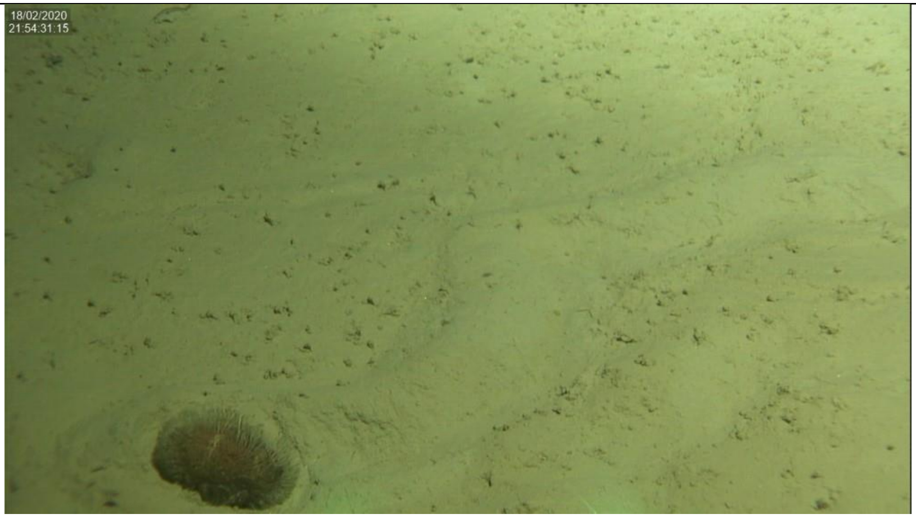
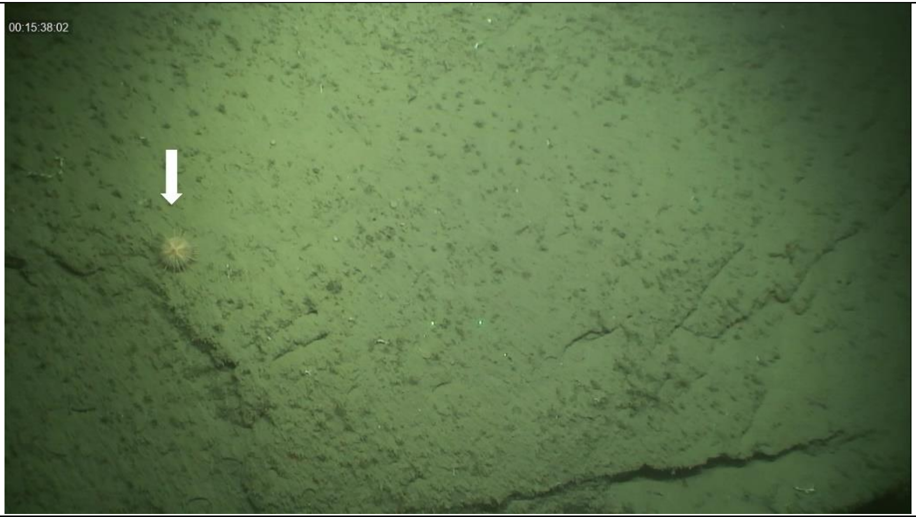
Phylum: Arthropoda Class: Malacostraca Familiy: Penaeidae AphiaID: 107109 *Parapenaeus longirostris* (Lucas, 1846)		1, 5, 7, 9, 10, 11, 12, 17, 18, 34, 35, 37, 40, 41, 43, 52
Phylum: Arthropoda Class: Malacostraca Familiy: Munididae AphiaID: 106835 *Munida* sp. Leach 1820		1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 21, 22, 23, 26, 28, 29, 30, 31, 33, 34, 35, 36, 37, 39, 41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 53, 54, 55, 56

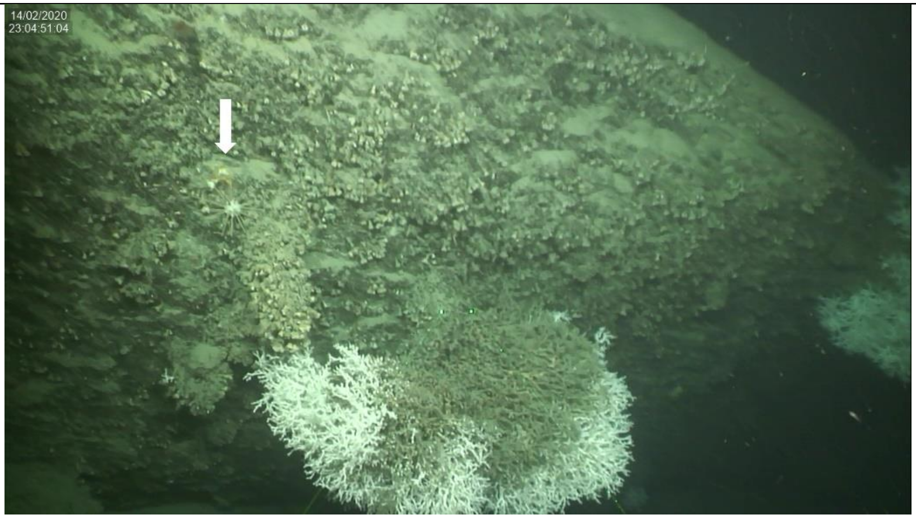
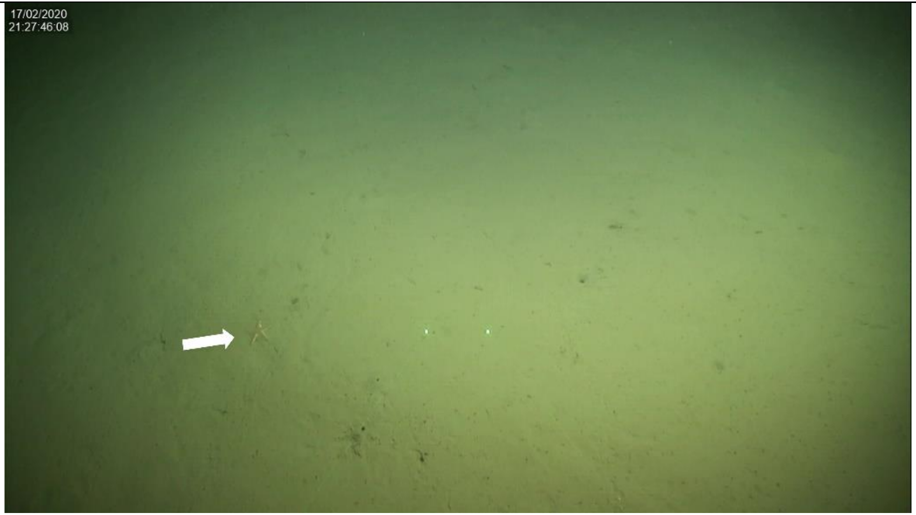
Phylum: Arthropoda Class: Malacostraca Familiy: Pandalidae AphiaID: 107654 *Plesionika acanthonotus* (Smith, 1882)		3, 4, 5, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 21, 22, 23, 26, 29, 30, 31, 32, 33, 34, 35, 37, 39, 40, 42, 43, 44, 45, 46, 48, 49, 50, 51, 52, 55, 56
Phylum: Arthropoda Class: Malacostraca Familiy: Pandalidae AphiaID: 107659 *Plesionika gigliolii* (Senna, 1902)		10, 11, 39, 42, 43, 55

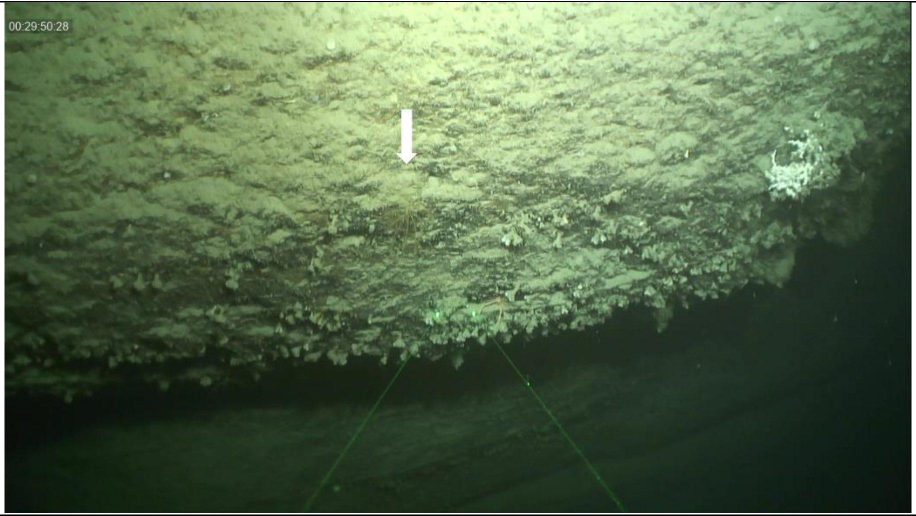
Phylum: Arthropoda Class: Malacostraca Familiy: Epialtidae AphiaID: 441513 *Anamathia rissoana* (Roux, 1828)		50
Phylum: Arthropoda Class: Malacostraca Familiy: Nephropidae AphiaID: 107254 *Nephrops norvegicus* (Linnaeus, 1758)		34, 40, 41, 48, 52, 55

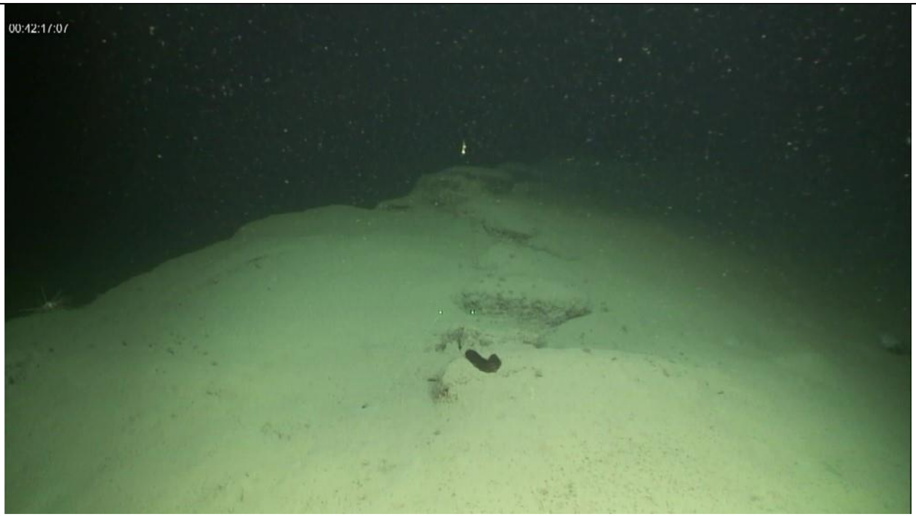
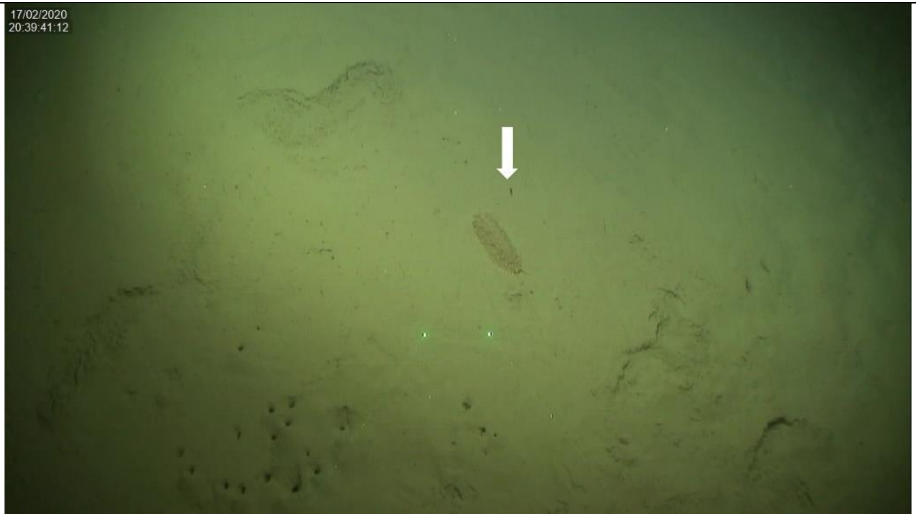
Phylum: Arthropoda Class: Malacostraca Familiy: Homolidae AphiaID: 107264 *Paromola cuvieri* (Risso, 1816)		2, 9, 13, 16, 22, 31, 56
Phylum: Arthropoda Class: Malacostraca Familiy: Polybiidae AphiaID: 107377 *Bathynectes maravigna* (Prestandrea, 1839)		3, 6, 7, 8, 9, 10, 11, 12, 17, 18, 22, 26, 27, 28, 30, 31, 36, 37, 40, 44, 46, 50, 51, 52

Phylum: Arthropoda Class: Malacostraca Familiy: Geryonidae AphiaID: 107372 cf. *Chaceon mediterraneus* Manning & Holthuis, 1989		56
Phylum: Arthropoda Class: Pycnogonida AphiaID: 1302 Pycnogonida Latreille, 1810		4, 10, 11, 12, 17

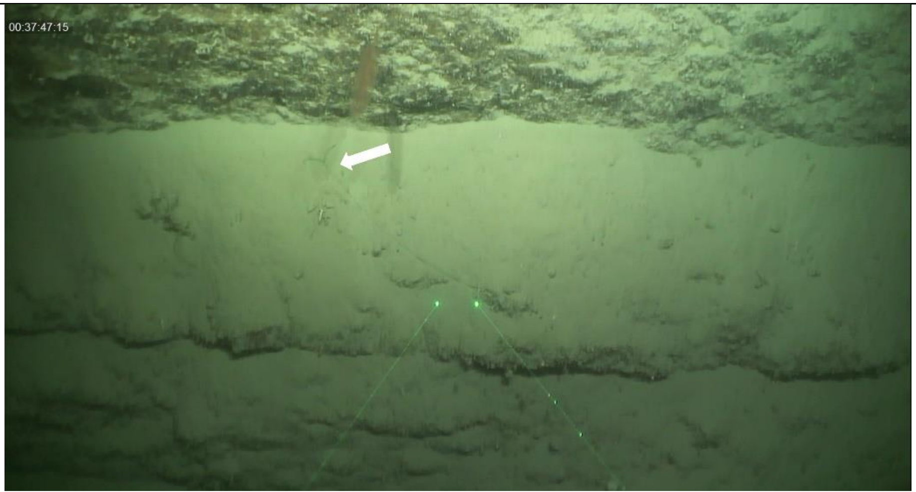
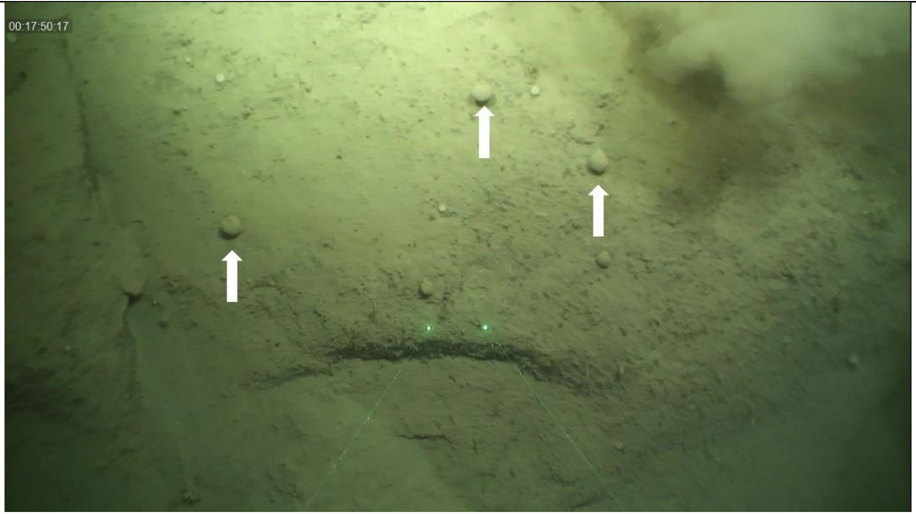
Phylum: Echinodermata Class: Echinoidea Familiy: Brissidae AphiaID: 124373 *Brissopsis lyrifera* (Forbes, 1841)		5, 10, 11, 12, 13, 22, 33, 42, 51
Phylum: Echinodermata Class: Echinoidea Familiy: Echinidae AphiaID: 532031 *Gracilechinus acutus* (Lamarck, 1816)		3, 4, 6, 8, 9, 11, 12, 16, 17, 18, 19, 21, 22, 23, 25, 26, 28, 29, 30, 31, 33, 35, 48, 49, 52, 56

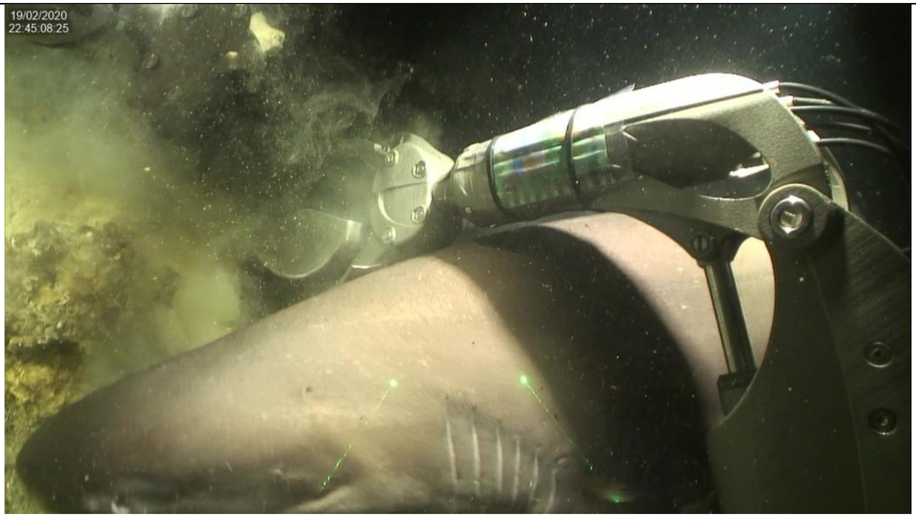
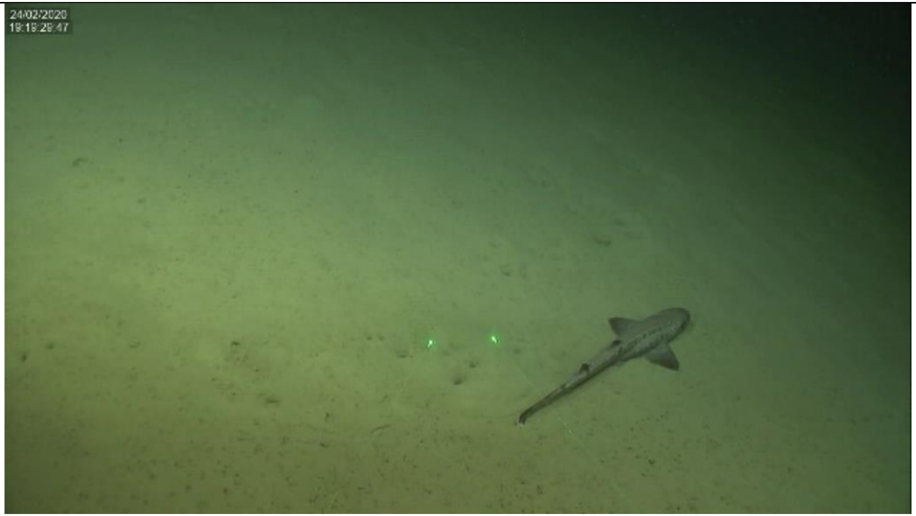
Phylum: Echinodermata Class: Echinoidea Familiy: Cidaridae AphiaID: 124257 *Cidaris cidaris* (Linnaeus, 1758)		1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 16, 17, 18, 23, 26, 28, 31, 34, 35, 36, 37, 38, 44, 49, 50
Phylum: Echinodermata Class: Asteroidea Familiy: Astropectinidae AphiaID: 123867 cf. *Astropecten irregularis* (Pennant, 1777)		4, 7

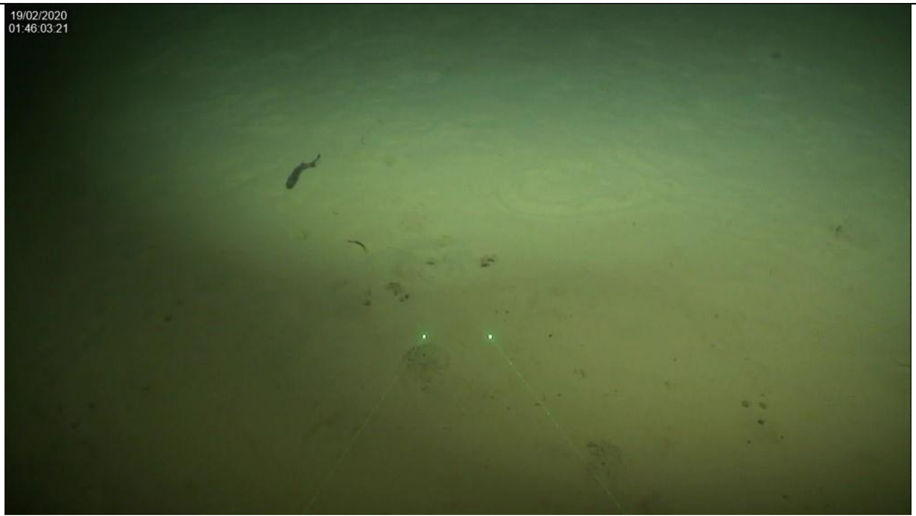
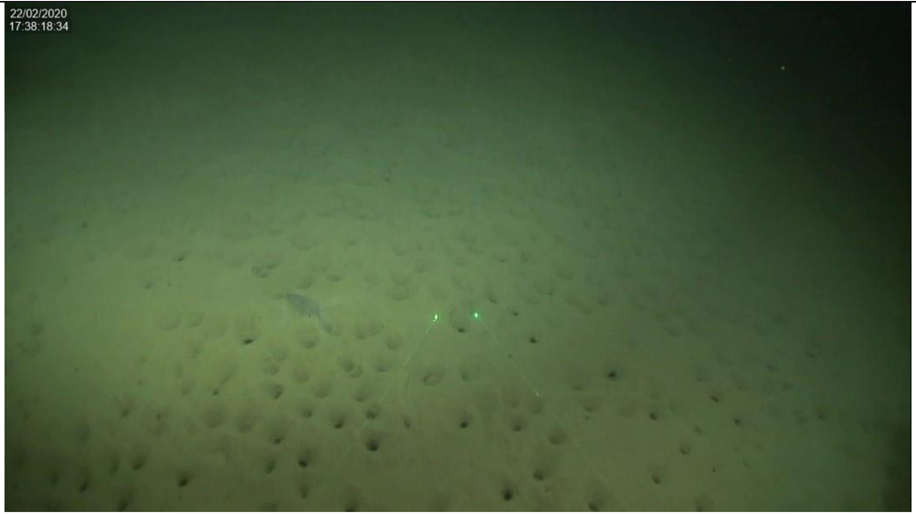
Phylum: Echinodermata Class: Asteroidea Familiy: Anseropodidae AphiaID: 123985 cf. *Anseropoda placenta* (Pennant, 1777)		6, 33, 56
Phylum: Echinodermata Class: Crinoidea Familiy: Antedonidae AphiaID: 124226 *Leptometra phalangium* (Maller, 1841)		1, 4, 5, 6, 7, 8, 9, 10, 12, 13, 18, 21, 28, 31, 33, 48

Phylum: Echinodermata Class: Holothuroidea Familiy: Holothuriidae AphiaID: 124501 *Holothuria (Panningothuria) forskali* Delle Chiaje, 1823		1, 4, 6
Phylum: Echinodermata Class: Holothuroidea Familiy: Stichopodidae AphiaID: 149898 cf. *Parastichopus regalis* (Cuvier, 1817)		3, 12

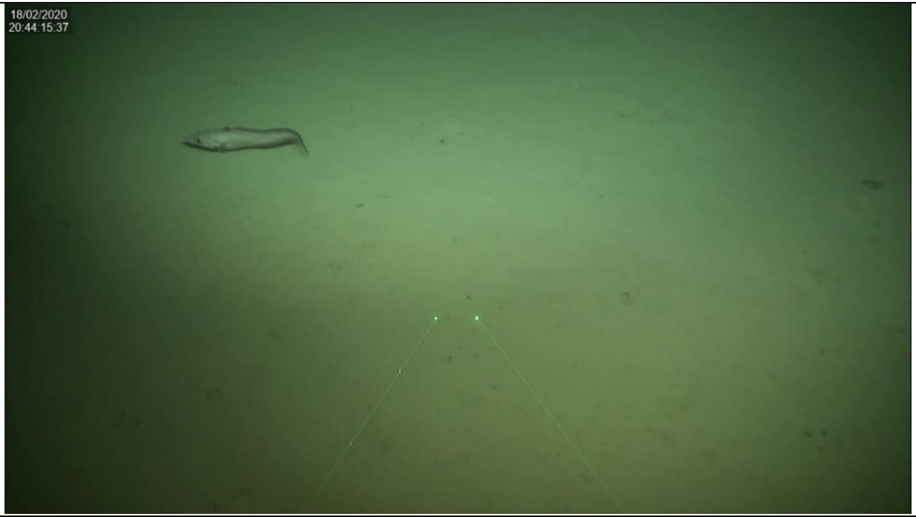
Phylum: Annelida Class: Polychaeta AphiaID: 883 Polychaeta sp.1 Grube, 1850		37, 46, 49
Phylum: Annelida Class: Polychaeta AphiaID: 883 Polychaeta sp.2 Grube, 1850		17, 48

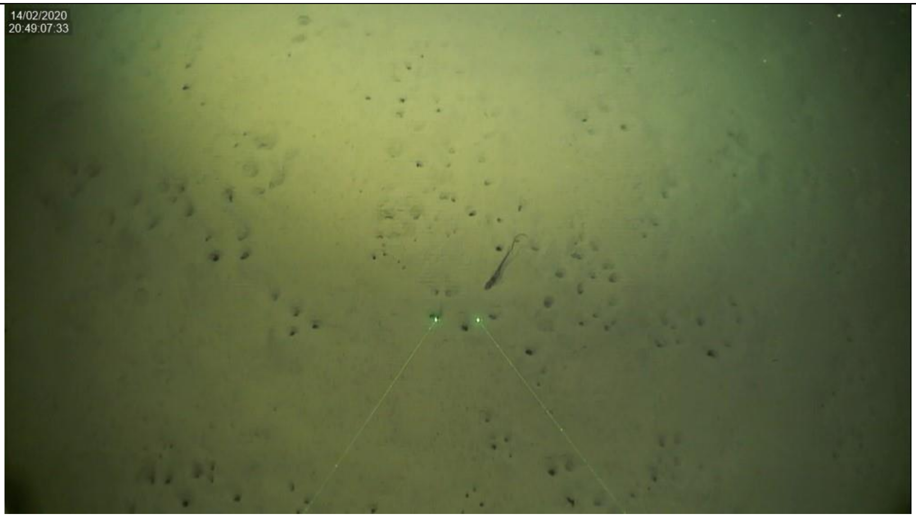
Phylum: Annelida Class: Polychaeta Family: Bonelliidae AphiaID: 110363 *Bonellia viridis* Rolando, 1822		4, 7, 8, 11, 14, 15, 16, 17, 18, 19, 21, 22, 23, 24, 26, 27, 28, 29, 30, 31, 33, 34, 35, 39, 41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 53, 55, 56
Phylum: Chordata Class: Ascidiacea Familiy: Octacnemidae AphiaID: 103751 *Dicopia antirrhinum* Monniot C., 1972		1, 2, 4, 5, 6, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 33, 34, 35, 37, 38, 39, 41, 42, 43, 44, 45, 46, 47, 48, 49, 50, 51, 52, 53, 54, 55, 56

Phylum: Chordata Class: Elasmobranchii Familiy: Hexanchidae AphiaID: 105833 *Hexanchus griseus* (Bonnaterre, 1788)		48
Phylum: Chordata Class: Elasmobranchii Familiy: Pentanchidae AphiaID: 105812 *Galeus melastomus* Rafinesque, 1810		7, 19, 24, 26, 45

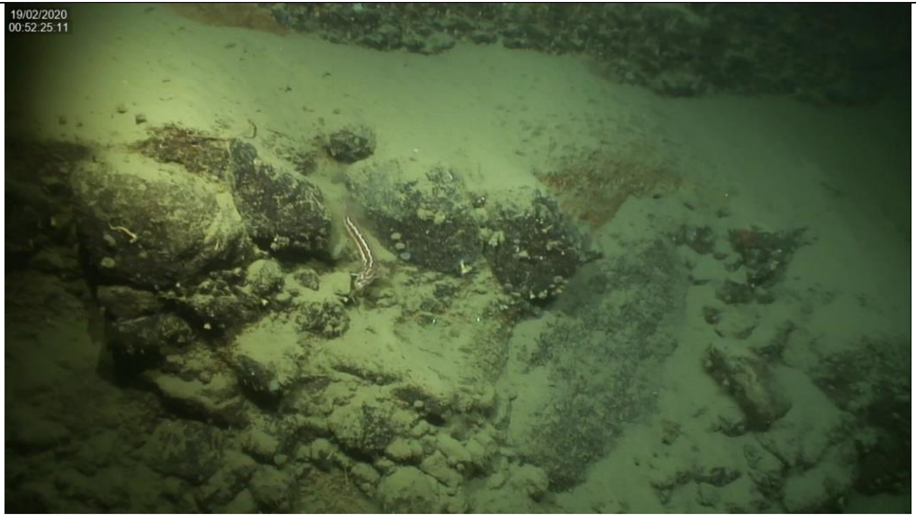
Phylum: Chordata Class: Elasmobranchii Familiy: Etmopteridae AphiaID: 105913 cf. *Etmopterus spinax* (Linnaeus, 1758)		10, 11, 12, 13
Phylum: Chordata Class: Teleostei Familiy: Scophthalmidae AphiaID: 127145 *Lepidorhombus boscii* (Risso, 1810)		43

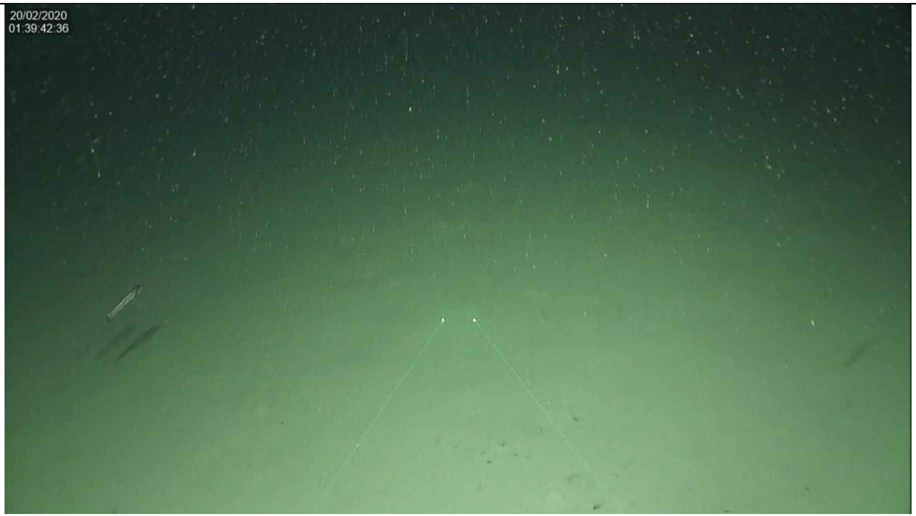
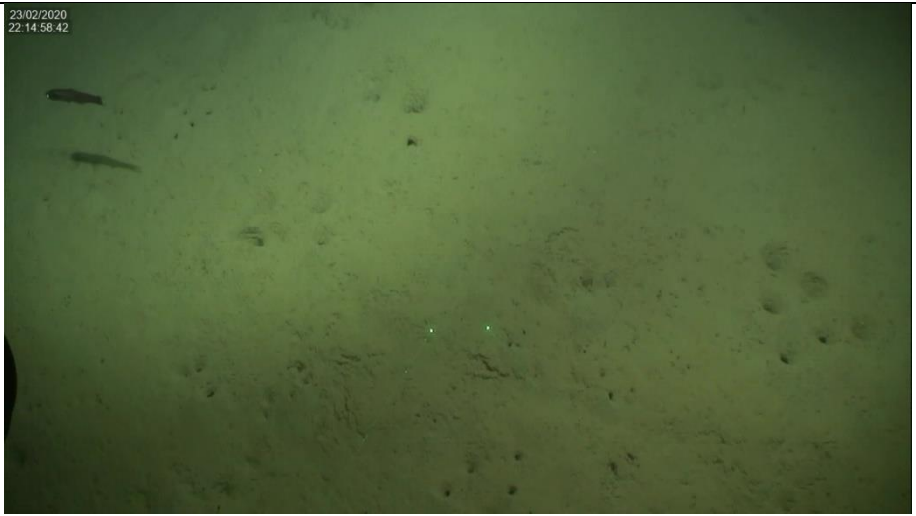
Phylum: Chordata Class: Teleostei Familiy: Notacanthidae AphiaID: 126642 *Notacanthus bonaparte* Risso, 1840		1, 2, 3, 4, 6, 7, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 21, 22, 23, 24, 26, 27, 28, 29, 30, 31, 33, 34, 35, 39, 40, 41, 43, 44, 45, 46, 47, 48, 49, 51, 52, 53, 56
Phylum: Chordata Class: Teleostei Familiy: Macrouridae AphiaID: 126473 *Nezumia aequalis* (Ganther, 1878)		2, 3, 5, 6, 9, 10, 13, 14, 16, 17, 18, 19, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 33, 34, 35, 36, 39, 40, 41, 44, 45, 47, 49, 50, 51, 52, 53, 55, 56

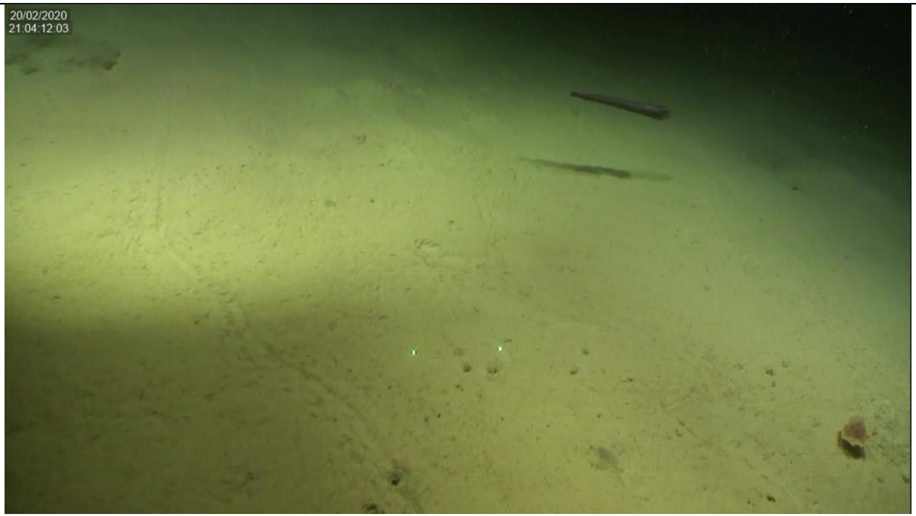
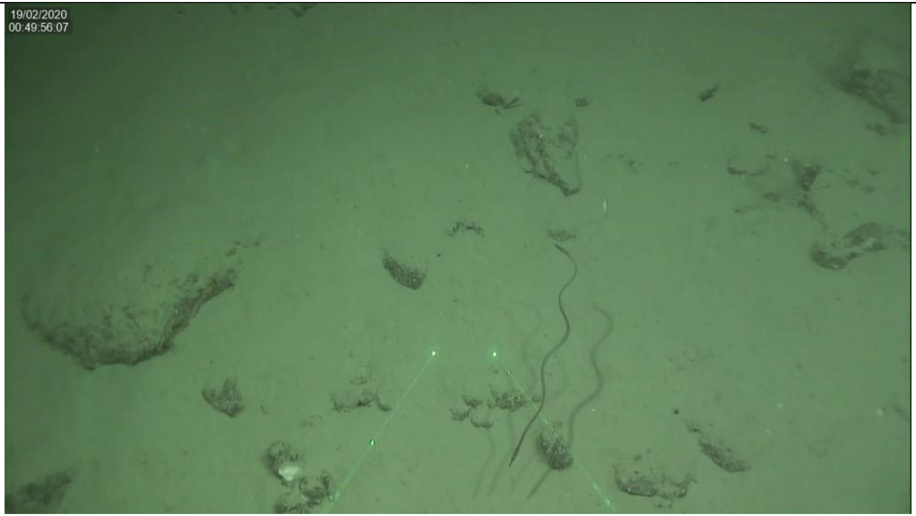
Phylum: Chordata Class: Teleostei Familiy: Macrouridae AphiaID: 398381 *Coelorinchus caelorhincus* (Risso, 1810)		1, 5, 9, 12, 14, 16, 17, 36, 37, 52
Phylum: Chordata Class: Teleostei Familiy: Macrouridae AphiaID: 126482 *Trachyrincus scabrus* (Rafinesque, 1810)		10, 11, 12, 16, 17, 19, 22, 23, 26, 28, 29, 30, 33, 41, 42, 49, 50, 52

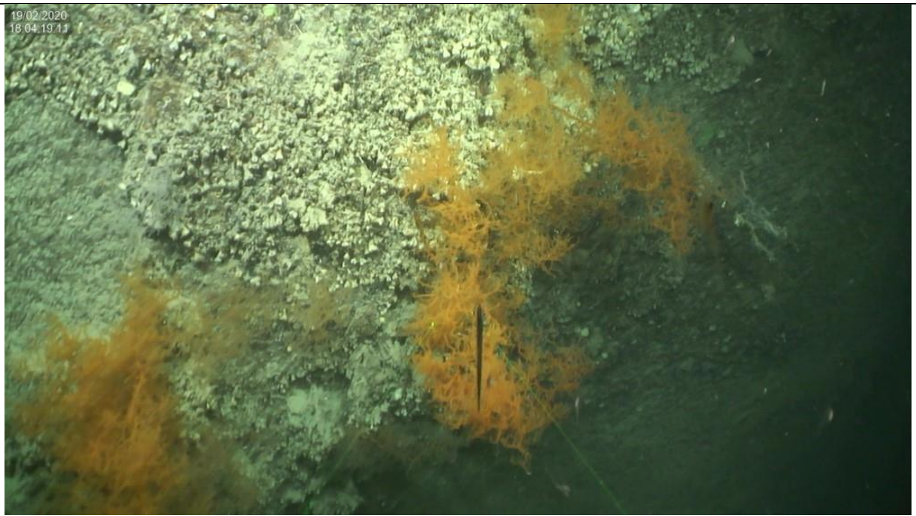
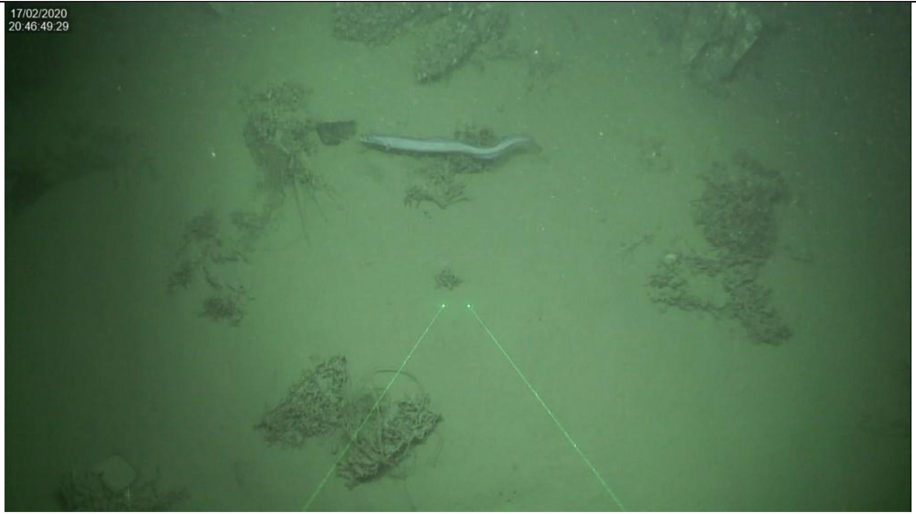
Phylum: Chordata Class: Teleostei Familiy: Macrouridae AphiaID: 158961 *Hymenocephalus italicus* Giglioli, 1884		1, 5, 8, 9, 11, 12, 16, 23, 24, 26, 27, 34, 35, 41, 42, 43, 45, 46, 47, 48, 51, 52, 53, 55, 56
Phylum: Chordata Class: Teleostei Familiy: Moridae AphiaID: 126495 *Lepidion lepidion* (Risso, 1810)		3, 11, 13, 15, 19, 22, 23, 24, 26, 28, 29, 30, 31, 32, 33, 34, 35, 44, 48, 51, 53, 54, 56

Phylum: Chordata Class: Teleostei Familiy: Phycidae AphiaID: 126501 *Phycis blennoides* (Brannich, 1768)		6, 9, 12, 16, 17, 18, 19, 23, 26, 27, 28, 30, 39, 41, 44, 45, 46, 49, 53
Phylum: Chordata Class: Teleostei Familiy: Gadidae AphiaID: 126439 *Micromesistius poutassou* (Risso, 1827)		35

Phylum: Chordata Class: Teleostei Familiy: Merlucciidae AphiaID: 126484 *Merluccius merluccius* (Linnaeus, 1758)		45
Phylum: Chordata Class: Teleostei Familiy: Lotidae AphiaID: 126454 *Gaidropsarus granti* (Regan, 1903)		10, 12, 16

Phylum: Chordata Class: Teleostei Familiy: Myctophidae AphiaID: 125498 Myctophidae Gill, 1893	 	17, 18, 42, 45, 49, 55
Phylum: Chordata Class: Teleostei Familiy: Myctophidae AphiaID: 125498 Myctophidae Gill, 1893	 	16

Phylum: Chordata Class: Teleostei Familiy: Stomiidae AphiaID: 125604 Stomiidae Bleeker, 1859		16, 19, 41, 48, 52
Phylum: Chordata Class: Teleostei Familiy: Serrivomeridae AphiaID: 126320 cf. *Serrivomer lanceolatoides* (Schmidt, 1916)		12, 17

Phylum: Chordata Class: Teleostei Familiy: Trichiuridae AphiaID: 127088 *Lepidopus caudatus* (Euphrasen, 1788)		15, 17, 18, 30, 34, 36, 37, 39, 40, 41, 42, 43, 44
Phylum: Chordata Class: Teleostei Familiy: Congridae AphiaID: 126285 *Conger conger* (Linnaeus, 1758)		3, 16, 26, 33, 34, 43, 51

Phylum: Chordata Class: Teleostei Familiy: Trachichthyidae AphiaID: 126404 *Hoplostethus mediterraneus* Cuvier, 1829		1, 4, 6, 7, 8, 9, 10, 12, 13, 14, 15, 16, 17, 18, 23, 24, 26, 27, 31, 34, 35, 37, 39, 40, 42, 43, 45, 48, 49, 50, 51, 52, 53
Phylum: Chordata Class: Teleostei Familiy: Polyprionidae AphiaID: 126998 *Polyprion americanus* (Bloch & Schneider, 1801)		44

Phylum: Chordata Class: Teleostei Familiy: Moridae AphiaID: 126497 *Mora moro* (Risso, 1810)		56

6.2.Appendix B: Supplementary materials of Chapter 4

Table 6.2. Statistical analysis of mortality data for the studied CWCs in the three suspended sediment concentration (SSC) treatments after 9 months of exposure.

CORAL	**RANDOM EFFECTS**				**FIXED EFFECTS**					
Species	**Groups**	**Name**	**Variance**	**SD**	**ID**	**Estimate**	**SE**	**z value**	**p**	
D. cornigera	Aquaria	Intercept	0.49	0.70	Intercept (Low SSC)	-2.15	0.69	-3.09	0.00	**
					Treatment High SSC	0.16	0.88	0.18	0.85	
D. pertusum	Aquaria	Intercept	0.53	0.73	Intercept	-3.51	0.58	-6.03	0.00	***

					Treatment Low SSC	1.59	0.70	2.26	0.02	*
					Treatment High SSC	1.85	0.68	2.71	0.00	**
M. oculata	Aquaria	Intercept	0.97	0.98	Intercept	-1.63	0.46	-3.48	0.00	***
					Treatment Low SSC	2.17	0.66	3.30	0.00	***
					Treatment High SSC	2.51	0.66	3.81	0.00	***
L. glaberrima	Aquaria	Intercept	0.00	0.00004	Intercept	-1.38	0.79	-1.75	0.08	
					Treatment Low SSC	0.98	1.02	0.96	0.33	
					Treatment High SSC	0.00005	1.11	0.00	1.00	

Table 6.3. Statistical analysis of growth rates for the studied CWCs in the three suspended sediment concentration (SSC) treatments after 9 months of exposure.

CORAL	**RANDOM EFFECTS**				**FIXED EFFECTS**						
Species		**Name**	**Variance**	**SD**	**ID**	**Value**	**SE**	**df**	**t-value**	**p**	
D. cornigera	Coral code	Intercept	0.41	0.64	Intercept	2.00	0.20	21	9.87	0.00	***
	Residual		0.00007	0.008	Time	0.00008	0.00001	69	6.22	0.00	***
					Treatment Low SSC	0.01	0.33	21	0.05	0.95	
					Treatment High SSC	0.10	0.30	21	0.33	0.74	
					Time : Treatment Low SSC	0.000007	0.00002	69	0.34	0.73	
					Time : Treatment High SSC	0.000005	0.00002	69	0.25	0.80	
D. dianthus	Coral code	Intercept	0.29	0.53	Intercept	2.25	0.17	26	13.212	0.00	***
	Residual		0.00001	0.003	Time	0.00002	0.000004	84	4.574	0.00	***
					Treatment Low SSC	0.10	0.24	26	0.422	0.67	
					Treatment High SSC	-0.18	0.24	26	-0.76	0.45	
					Time : Treatment Low SSC	0.000005	0.000006	84	-0.88	0.38	
					Time : Treatment High SSC	0.00001	0.000006	84	1.81	0.07	
D. pertusum	Coral code	Intercept	0.30	0.55	Intercept	1.95	0.19	16	9.99	0.00	***
	Residual		0.00002	0.005	Time	0.00005	0.000008	54	5.80	0.00	***
					Treatment Low SSC	-0.45	0.31	16	-1.45	0.16	
					Treatment High SSC	-0.11	0.29	16	-0.37	0.71	

					Time : Treatment Low SSC	-0.00002	0.00001	54	-1.60	0.11	
					Time : Treatment High SSC	0.0000006	0.00001	54	0.04	0.96	
M. oculata	Coral code	Intercept	0.47	0.69	Intercept	1.57	0.39	3	3.93	0.02	*
	Residual		0.000007	0.002	Time	0.00006	0.000007	13	7.73	0.00	***
					Treatment Low SSC	0.11	0.63	3	0.17	0.87	
					Time : Treatment Low SSC	-0.00002	0.00001	13	-1.80	0.09	
M. lepida	Coral code	Intercept	0.10	0.32	Intercept	2.85	0.10	27.28	27.98	0.00	***
	Residual		0.0008	0.02	Time	0.00009	0.00005	57	1.74	0.08	
					Treatment Low SSC	0.02	0.14	27.28	0.19	0.84	
					Treatment High SSC	0.007	0.14	27.28	0.05	0.96	
					Time : Treatment Low SSC	-0.0001	0.00007	57	-1.38	0.17	
					Time : Treatment High SSC	-0.00009	0.00007	57	-1.28	0.20	

Table 6.4. Statistical analysis of respiration for the studied CWCs in the three suspended sediment concentration (SSC) treatments after 4 and 9 months of exposure.

CORAL	**RANDOM EFFECTS**				**FIXED EFFECTS**						
Species		**Name**	**Variance**	**SD**	**ID**	**Value**	**SE**	**df**	**t-value**	**p**	
D. cornigera	Coral code	Intercept	0.67	0.82	Intercept	2.91	0.50	41.61	5.80	0.00	***
	Residual		0.47	0.68	Time	-0.02	0.06	21.70	-0.37	0.71	

					Treatment Low SSC	-0.30	0.74	41.23	-0.41	0.68	
					Treatment High SSC	0.25	0.73	41.51	0.34	0.73	
					Time : Treatment Low SSC	-0.03	0.09	23.31	-0.36	0.72	
					Time : Treatment High SSC	-0.07	0.09	22.15	-0.76	0.45	
D. dianthus	Coral code	Intercept	0.62	0.79	Intercept	2.10	0.35	52.94	5.97	0.00	***
	Residual		0.15	0.39	Time	-0.01	0.03	27	-0.40	0.68	
					Treatment Low SSC	0.29	0.49	52.94	0.6	0.55	
					Treatment High SSC	0.27	0.49	52.94	0.55	0.58	
					Time : Treatment Low SSC	-0.02	0.05	27	-0.39	0.69	
					Time : Treatment High SSC	-0.02	0.05	27	-0.59	0.56	
D. pertusum	Coral code	Intercept	0.84	0.91	Intercept	2.78	0.52	38.88	5.31	0.00	***
	Residual		0.47	0.68	Time	-0.03	0.06	18.74	-0.50	0.62	
					Treatment Low SSC	0.02	0.76	38.01	0.02	0.98	
					Treatment High SSC	1.41	0.75	38.33	1.86	0.07	
					Time : Treatment Low SSC	-0.06	0.10	20.41	-0.60	0.55	
					Time : Treatment High SSC	-0.23	0.10	19.88	-2.32	0.03	*
M. oculata	Coral code	Intercept	2.62	1.61	Intercept	4.75	0.57	27.71	8.23	0.00	***

	Residual		0.12	0.35	Time	-0.17	0.04	4.13	-3.54	0.02	*
					Treatment Low SSC	1.04	0.84	26.63	1.23	0.22	
					Treatment High SSC	-0.46	0.81	24.20	-0.56	0.57	
					Time : Treatment Low SSC	-0.29	0.08	4.16	-3.41	0.02	*
L. glaberrima	Coral code	Intercept	0.07	0.28	Intercept	0.50	0.13	13.86	3.68	0.00	***
	Residual		0.006	0.08	Time	-0.003	0.01	2.92	-0.27	0.80	
					Treatment Low SSC	-0.12	0.20	13.75	-0.60	0.55	
					Treatment High SSC	-0.21	0.20	11.05	-1.01	0.33	
					Time : Treatment Low SSC	-0.002	0.02	2.94	-0.09	0.93	
M. lepida	Coral code	Intercept	0.05	0.23	Intercept	1.08	0.10	52.58	10.69	0.00	***
	Residual		0.01	0.11	Time	-0.04	0.01	27	-4.24	0.00	***
					Treatment Low SSC	-0.05	0.14	52.58	-0.35	0.72	
					Treatment High SSC	0.09	0.14	52.58	0.66	0.50	
					Time : Treatment Low SSC	-0.01	0.01	27	-0.58	0.56	
					Time : Treatment High SSC	-0.02	0.14	27	-1.61	0.11	

Table 6.5. Statistical analysis of excretion for the studied CWCs in the three suspended sediment concentration (SSC) treatments after 4 and 9 months of exposure.

CORAL	**RANDOM EFFECTS**				**FIXED EFFECTS**						
Species		**Name**	**Variance**	**SD**	**ID**	**Value**	**SE**	**df**	**t-value**	**p**	
D. cornigera	Coral code	Intercept	0.005	0.07	Intercept	0.07	0.12	21.95	0.58	0.56	
	Residual		0.009	0.09	Time	0.003	0.01	16.84	0.19	0.84	
					Treatment Low SSC	0.13	0.16	21.95	0.80	0.42	
					Treatment High SSC	0.05	0.14	21.73	0.42	0.68	
					Time : Treatment Low SSC	-0.02	0.02	16.84	-0.93	0.36	
					Time : Treatment High SSC	0.0004	0.01	16.12	0.02	0.98	
D. dianthus	Coral code	Intercept	0.0001	0.01	Intercept	0.02	0.03	23.93	0.81	0.42	
	Residual		0.001	0.03	Time	0.00007	0.005	21.34	0.01	0.98	
					Treatment Low SSC	0.02	0.04	25.98	0.60	0.55	
					Treatment High SSC	0.09	0.04	19.62	2.10	0.04	*
					Time : Treatment Low SSC	-0.003	0.007	22.54	-0.43	0.67	
					Time : Treatment High SSC	-0.009	0.006	15.76	-1.41	0.17	
D. pertusum	Coral code	Intercept	0.002	0.05	Intercept	-0.001	0.05	21.55	-0.021	0.98	
	Residual		0.003	0.05	Time	0.01	0.006	14.89	2.32	0.03	*
					Treatment Low SSC	0.29	0.08	27.49	3.36	0.002	**
					Treatment High SSC	0.06	0.07	21.65	0.93	0.36	
					Time : Treatment Low SSC	-0.03	0.01	24.57	-2.80	0.009	**

					Time : Treatment High SSC	-0.01	0.01	15.16	-1.37	0.19	
M. oculata	Coral code	Intercept	0.01	0.13	Intercept	0.30	0.08	8.23	3.57	0.006	**
	Residual		0.008	0.09	Time	-0.005	0.01	4.19	-0.408	0.70	
					Treatment Low SSC	-0.06	0.14	6.42	-0.43	0.68	
					Treatment High SSC	-0.02	0.09	22.34	-0.25	0.80	
					Time : Treatment Low SSC	-0.006	0.02	3.92	-0.25	0.81	
L.glaberrima					Intercept	0.005	0.01		0.35	0.73	
					Time	0.001	0.002		-0.56	0.59	
					Treatment Low SSC	.016	0.01		1.29	0.25	
M. lepida	Coral code	Intercept	0.00003	0.005	Intercept	0.02	0.01	34.29	1.3	0.20	
	Residual		0.0001	0.01	Time	0.0001	0.002	29.19	0.05	0.95	
					Treatment Low SSC	-0.0005	0.02	32.56	-0.026	0.98	
					Treatment High SSC	0.03	0.02	32.35	1.77	0.08	
					Time : Treatment Low SSC	-0.0005	0.002	25.75	-0.22	0.82	
					Time : Treatment High SSC	-0.005	0.002	25.53	-2.09	0.046	*

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