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Coral habitats in submarine canyons of the Bay of Biscay: distribution, ecology and vulnerability

Habitats coralliens dans les canyons sous-marins du Golfe
de Gascogne : distribution, écologie et vulnérabilité



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Introduction

Introduction (version française)

1. Les coraux d'eau froide : cibles prioritaires de conservation

Les coraux d'eau froide sont définis comme les cnidaires qui ont un squelette ou des éléments de squelette carbonaté ou protéique (Cairns, 2007). Cependant, ce terme masque une hétérogénéité de taxons qui répondent à cette définition et appartiennent à différents niveaux et groupes taxonomiques : la sous-classe Octocorallia (incluant les ordres Alcyonacea et Pennatulacea), les ordres Antipatharia et Scleractinia, les familles d'hydrozoaires Stylasteridae et Milleporidae, ainsi que quelques espèces de Zoanthidae et d'Hydractiniidae calcifiées (Cairns, 2007). La majorité de ces coraux ont besoin de substrat dur pour se développer, à l'exception des certains antipathaires, la famille de gorgones Isididae et la plupart de pennatules (Roberts *et al.*, 2009 ; Wagner *et al.*, 2012 ; Williams, 2011).

Les coraux d'eau froide ont été observés dans tous les océans entre 40 et plus de 5000 m de profondeur (Freiwald *et al.*, 2004 ; Wagner *et al.*, 2012 ; Williams, 2011). Ils peuvent former des habitats, par exemple les récifs et jardins de coraux (Freiwald *et al.*, 2004 ; Roberts *et al.*, 2009 ; Roberts *et al.*, 2006). Ces habitats ont un rôle écologique important, particulièrement les récifs de *Lophelia pertusa* et/ou *Madrepora oculata* ; ils fonctionnent comme des zones d'alimentation et de reproduction, des nurseries et ils fournissent des refuges à d'autres organismes (Buhl-Mortensen *et al.*, 2010 ; Roberts *et al.*, 2009). La structure tridimensionnelle des coraux d'eau froide crée une hétérogénéité qui pourrait favoriser la biodiversité et la biomasse des communautés benthodémersales (Buhl-Mortensen *et al.*, 2010 ; Roberts *et al.*, 2006).

Les espèces coralliennes d'eau froide sont sensibles ou vulnérables aux activités humaines, comme la pêche, l'industrie pétrolière et les déchets marins, parce qu'ils sont fragiles, ont une grande longévité et des taux de croissance faibles qui se traduisent par une résilience faible (par ex. Clark *et al.*, 2016 ; Grehan *et al.*, 2005 ; Ramirez-Llodra *et al.*, 2011 ; Roberts *et al.*, 2006). Les menaces qui pèsent sur les coraux d'eau froide et le rôle structurant de ces habitats les identifient comme des cibles prioritaires de préservation. En effet, les coraux d'eau froide sont listés comme espèces ou habitats vulnérables, menacés ou en déclin par plusieurs initiatives internationales et européennes, par exemple le Conseil International pour l'Exploration de la Mer (CIEM), la convention d'Oslo-Paris (OSPAR) et la Directive Habitats Faune Flore de la Commission Européenne (par ex. EEC, 1992 ; FAO, 2009 ; OSPAR, 2008).

La planification spatiale est un outil privilégié de la gestion des écosystèmes marins vulnérables ; cependant, des études récentes indiquent que la limitation majeure pour la création d'un réseau cohérent d'aires marines protégées est le manque d'information détaillée sur la distribution et l'écologie de coraux d'eau froide (par ex. Auster *et al.*, 2011 ; Davies *et al.*, 2007 ; Davies *et al.*, 2015). Une meilleure compréhension de la distribution des habitats coralliens, leur contrôle environnemental, les communautés de faune associée ainsi que la connectivité et la dispersion des espèces, sont essentiels pour contribuer à cet objectif.

La recherche sur des coraux d'eau froide et leurs habitats a longtemps été biaisée géographiquement, avec un effort particulier en Atlantique nord-est, et taxonomiquement, avec un accent sur les scléractiniaires récifaux *L. pertusa* et *M. oculata*. Cependant, le nombre d'études portant sur d'autres régions géographiques et sur d'autres espèces coralliennes a récemment augmenté. Si les récifs coralliens ont une biodiversité élevée par rapport aux habitats non-coralliens (Buhl-Mortensen *et al.*, 2010 ; Henry et Roberts, 2007 ; Mortensen *et al.*, 1995), les premières études incluant des habitats coralliens de substrat meuble suggèrent que la diversité de la communauté y est faible (Davies *et al.*, 2014 ; Robert *et al.*, 2015). D'une manière générale cependant, le rôle structurant des coraux non-récifaux a été peu étudié et est encore mal connu en environnement profond.

2. Les canyons sous-marins favorables aux habitats coralliens

Les coraux d'eau froide sont capables de coloniser un nombre des structures géologiques, comme les monts sous-marins, les rebords du plateau continental et les canyons sous-marins (Freiwald *et al.*, 2004).

Les canyons sous-marins incisent un grand nombre de plateaux continentaux (Harris et Whiteway, 2011) et y ont un rôle écologique important (Fernandez-Arcaya *et al.*, 2017 : Annexe I). La topographie complexe des canyons crée des régimes hydrodynamiques et de sédimentation spécifiques qui exposent le substrat dur (De Leo *et al.*, 2010). L'interaction entre l'hydrodynamisme, par exemple les forts courants de marée, et les taux de sédimentation crée une hétérogénéité importante des substrats dans les canyons sous-marins, incluant des zones d'érosion et des zones de dépôt de sédiment. Les canyons également augmentent le processus de mélange vertical des masses d'eau, surtout au niveau de la tête de canyon, et l'enrichissement en nutriments des eaux de surface augmente la croissance phytoplanctonique (Huthnance, 1995). Cette production primaire serait véhiculée dans les canyons sous-marins qui se comportent comme un conduit pour le transport de la matière organique (Amaro *et al.*, 2015 ; Amaro *et al.*, 2016 ; De Leo *et al.*, 2010).

La topographie, l'hydrodynamisme, les patrons de sédimentation et les apports trophiques propres aux canyons sous-marins favorisent la présence de coraux d'eau froide et la formation des habitats construits par ces organismes (par ex. De Leo *et al.*, 2010 ; Mortensen et Buhl-Mortensen, 2005).

La pente continentale du Golfe de Gascogne est dominée par des canyons sous-marins. L'occurrence de coraux d'eau froide est connue dans ce bassin depuis la fin du 19^e siècle, mais la connaissance de leur distribution est très limitée. Le premier rapport sur ces coraux d'eau froide était destiné à alerter des risques que présentaient ces « coraux de mer profonde nuisibles aux chalutiers » (Joubin, 1922). Depuis, peu d'études ont exploré la distribution des coraux d'eau froide dans le Golfe de Gascogne (De Mol *et al.*, 2011 ; Le Danois, 1948 ; Reveillaud *et al.*, 2008 ; Zibrowius, 1980).

La pêche et les déchets marins sont deux pressions d'origine anthropiques connues dans le Golfe de Gascogne (par ex. Berthou *et al.*, 2014 ; Galgani *et al.*, 2000 ; Joubin, 1922 ; Pham *et*

al., 2014). Cependant, les mesures de gestion environnementale sont rares et ne concernent pas les habitats benthiques.

Le manque de connaissance sur la distribution des coraux d'eau froide dans ce bassin limite le développement d'une stratégie de préservation de ces écosystèmes vulnérables. Il est donc nécessaire de comprendre la distribution des habitats coralliens afin d'apporter une expertise scientifique à la mise en place de mesures de préservation de ces habitats.

3. Le projet de CoralFISH et la collection de données

Le développement des outils de préservation des habitats coralliens était une des finalités du projet européen CoralFISH (financement FP7, convention de subvention no. 213144, 2008-2012). Ce projet cherchait à évaluer les interactions entre coraux d'eau froide, les populations de poissons et les activités de pêche pour développer des outils de suivi et des modèles prédictifs qui favoriseraient une gestion écosystémique (<http://eu-fp7-coralfish.net/>).

Compte tenu du manque de connaissance sur la distribution des coraux dans le Golfe de Gascogne, l'acquisition de données était un prérequis aux objectifs de gestion.

Trois campagnes océanographiques (BobGeo, BobGeo 2 et BobEco) ont fait partie du projet CoralFISH et récolté des données sur des habitats coralliens, particulièrement sur les scléractiniaires récifaux *L. pertusa* et *M. oculata*, par une caméra tractée Scampi (BobGeo) ou un *Remotely Operated Vehicle* (ROV Victor ; BobEco). Des données complémentaires ont été récoltées de façon opportuniste par la caméra tractée pendant quatre campagnes supplémentaires (Evhoe). J'ai participé à la campagne BobEco et à une campagne d'Evhoe (Evhoe 2013). Au total, 24 canyons ont été explorés pendant 46 plongées afin d'examiner la distribution et l'écologie des habitats coralliens et de leur communautés (Fig. 1).

Un système de classification des habitats coralliens a été développé pendant le projet CoralFISH (Davies *et al.*, 2017 : Annexe II). Cette classification inclut 15 biotopes ou habitats décrits par le ou les espèces de corail/coraux dominant(s) ainsi que le type de substrat dominant. Cette classification est à la base de notre étude et a guidé l'analyse des images acquises par le ROV et la caméra tractée.

4. Les objectifs de thèse

Cette thèse vise à améliorer la connaissance et la compréhension de la distribution, la diversité et les fonctions des habitats coralliens dans le Golfe de Gascogne, avec comme finalité de fournir une base scientifique solide au développement des stratégies de préservation de ces habitats vulnérables. Quatre objectifs scientifiques ont été définis :

1. Décrire l'hétérogénéité et la diversité des habitats coralliens associés aux canyons sous-marins du Golfe de Gascogne.

2. Déterminer les facteurs qui influencent la distribution des habitats coralliens à différentes échelles spatiales.
3. Décrire la structure et la composition des communautés de mégafaune associées aux habitats coralliens et identifier les facteurs abiotiques et biotiques déterminants.
4. Décrire la nature et la distribution des déchets et évaluer leurs impacts potentiels sur les habitats coralliens du Golfe de Gascogne.

Le **premier chapitre** est une synthèse des connaissances sur les canyons sous-marins et coraux d'eau froide.

Le **deuxième chapitre** décrit les contextes géologiques et océanographiques du Golfe de Gascogne, avec un accent sur les facteurs qui pourraient favoriser le développement des habitats coralliens.

Le **troisième chapitre** est un article publié dans *Frontiers in Marine Science* (Van den Beld *et al.*, 2017). Il répond aux deux premiers objectifs de cette étude. La distribution des habitats coralliens et la composition des assemblages de coraux dans les canyons sous-marins du Golfe de Gascogne sont décrites. Les déterminants abiotiques de la distribution des habitats sont recherchés parmi les facteurs géographiques, géomorphologiques et océanographiques. Les questions principales sont : (1) Quelles sont la nature et la diversité des habitats coralliens profonds, et (2) Quelle est la distribution spatiale, aux échelles régionale et locale, de ces habitats coralliens ? Nous avons émis l'hypothèse que la distribution des habitats est contrainte par le régime hydrodynamique et les patrons de sédimentation tant à l'échelle régionale (le Golfe de Gascogne) qu'à l'échelle du canyon. Le type de substrat, un résultat de l'interaction entre hydrodynamisme et sédimentation, est un facteur important qui contrôle la distribution. Plus spécifiquement, le flanc nord-est, exposé au courant dominant, serait plus propice au développement des coraux d'eau froide. En outre, nous avons recherché à confirmer les observations de De Mol *et al.* (2011) qui rapportaient la présence de scléractiniaires vivants en deçà de 350 m de profondeur et des débris de scléractiniaires à des profondeurs inférieures à 350 m.

Le **quatrième chapitre** est un manuscrit en préparation qui décrit les communautés de mégafaune associées aux habitats coralliens et répond au troisième objectif. L'abondance et la diversité des espèces non-coralliennes associées aux habitats coralliens sont évaluées. La composition taxonomique est également décrite. En outre, les influences des facteurs abiotiques, comme le type de substrat dominant ainsi que celle des facteurs biotiques, comme la densité ou le taux de couverture des coraux, sont explorées. Les questions principales posées sont : (1) Est-ce que les habitats coralliens, définis *a priori* par leurs espèces dominantes et le substrat, diffèrent par la structure et la composition de la faune associée ? et (2) Les récifs de coraux se caractérisent-ils par une diversité plus élevée (i.e. '*biodiversity hotspot*') que les autres habitats coralliens ?

Le **cinquième chapitre** (Van den Beld *et al.*, 2016) décrit la distribution des déchets dans les canyons sous-marins du Golfe de Gascogne. Ce chapitre répond au quatrième objectif de cette

thèse. Le chapitre donne une description des déchets observés sur des images dans les canyons sous-marins du Golfe de Gascogne. L'influence du relief du fond marin en particulier celui créé par les structures géologiques et biologiques est évaluée. L'origine et l'impact potentiels des déchets sont discutés.

Une conclusion générale résume les résultats principaux de la thèse, suivie des perspectives présentant :

1. L'effort et stratégie d'échantillonnage recommandés afin de compléter au mieux nos connaissances sur les habitats coralliens du Golfe de Gascogne.
2. Les apports, limites et perspectives à court terme de la modélisation prédictive d'habitats avec le jeu de données existant.
3. Les implications de ce travail pour la conservation et les applications directes auxquelles elle a contribué en termes de proposition de grands secteurs Natura 2000.

Trois autres articles scientifiques avec une contribution comme co-auteur sont présentés en annexe :

Annex I. revue sur le rôle écologique des canyons par Fernandez-Arcaya *et al.* Cet article est **publié** dans le volume spécial *Horizon Scan 2017 : Emerging Issues in Marine Science* de la revue scientifique *Frontiers in Marine Science* (Fernandez-Arcaya *et al.*, 2017).

Annex II. article sur le système de la classification développé pendant le projet CoralFISH par Davies *et al.* Cet article est **sous-pressé** dans le volume spécial CoralFISH qui paraîtra dans la revue *Deep-Sea Research II* (Davies *et al.*, 2017).

Annex III. article qui rapporte la co-occurrence de *L. pertusa* et *M. oculata* dans les canyons sous-marins du Golfe de Gascogne par Arnaud-Haond *et al.* Cet article est **sous-pressé** dans le volume spécial CoralFISH qui paraîtra dans la revue *Deep-Sea Research II* (Arnaud-Haond *et al.*, 2015).

Ce manuscrit est bilingue. L'introduction, les conclusions générales et les perspectives sont en français et en anglais. Les chapitres sont rédigés en anglais, mais débutent avec un résumé du chapitre en français.

Introduction (English version)

1. Cold-water corals as conservation targets

Cold-water corals are defined as cnidarians that have a skeleton or parts of the skeleton made by calcium carbonate or have a black, horn-like proteinaceous skeleton (Cairns, 2007). However, this term masks the heterogeneity of taxa that meet this definition belonging to different taxonomic levels: the **subclass** Octocorallia (including Alcyonacea and Pennatulacea), the **orders** Antipatharia and Scleractinia, the hydrozoan **families** Stylasteridae and Milleporidae, as well as some zoanthid and calcified hydractiniids **species** (Cairns, 2007). Most of these corals need hard substrate to settle, with the exception of a few antipatharians, the gorgonian family Isididae and most sea pens (Roberts *et al.*, 2009; Wagner *et al.*, 2012; Williams, 2011). Cold-water corals are observed in every ocean and reported from 40 m to more than 5000 m water depth (Freiwald *et al.*, 2004; Wagner *et al.*, 2012; Williams, 2011). They can form habitats, e.g. reefs and coral gardens (Freiwald *et al.*, 2004; Roberts *et al.*, 2009; Roberts *et al.*, 2006). These habitats have an important ecological role, especially *Lophelia pertusa*/*Madrepora oculata* reefs; they serve as feeding, reproduction and nursery grounds and they provide shelter for other organisms (Buhl-Mortensen *et al.*, 2010; Roberts *et al.*, 2009). The three-dimensional structure of cold-water coral habitats creates a heterogeneity that locally enhances the biodiversity and biomass of benthic-demersal communities (Buhl-Mortensen *et al.*, 2010; Roberts *et al.*, 2006).

Cold-water coral species are vulnerable to human activities, such as the fishing and the oil and gas industries and marine litter, because they are fragile, long-lived and have slow growth rates which translates into a low resistance (e.g. Clark *et al.*, 2016; Grehan *et al.*, 2005; Ramirez-Llodra *et al.*, 2011; Roberts *et al.*, 2006). The threats to cold water corals and the engineering role of these species that may enhance the biomass and biodiversity raised them as priority targets for conservation. Indeed, cold-water corals are recognised as important to conserve and protect by several international and European initiatives, e.g. the International Council for the Exploration of the Sea (ICES), the Oslo-Paris Convention (OSPAR) and the European Commission's (EC) Habitats Directive, and could therefore feed into local and regional marine management plans. These initiatives have set up criteria such as rarity, sensitivity or vulnerability to select conservation targets (e.g. EEC, 1992; FAO, 2009; OSPAR, 2008). *Lophelia* reefs and cold-water coral gardens are examples of habitats falling under one or more of these initiatives.

To conserve cold-water corals habitats, it is necessary to establish a network of marine protected areas and potential other regulations. However, recent studies pointed out that the most important issue in establishing a good marine protected area network is the lack of detailed information about the distribution and ecology of cold-water corals (e.g. Auster *et al.*, 2011; Davies *et al.*, 2007; Davies *et al.*, 2015). A better understanding about the distribution of different coral habitats, their environmental drivers, and the faunal community associated with these coral habitats as well as the connectivity and dispersal of corals and associated fauna is essential for this goal.

The research focussing on cold-water corals and their habitats is geographically-biased, especially the North-East Atlantic, and species-biased, with a focus on the reef-forming scleractinians *L. pertusa* and *M. oculata*. However, the number of studies in other regions of the world and to habitats formed by other cold-water corals is recently increasing. Coral reefs have a high biodiversity compared to non-coral habitats (Buhl-Mortensen *et al.*, 2010; Henry and Roberts, 2007; Mortensen *et al.*, 1995). Conversely, a low diversity was observed for the community of coral habitats dominated by soft sediment in three submarine canyons (Davies *et al.*, 2014; Robert *et al.*, 2015). The engineering role of non-reef-forming corals and the diversity of the habitat they form are, however, unclear.

2. Submarine canyons as hosts for coral habitats

Cold-water corals are able to colonise many geomorphic features, such as seamounts, along the edges of the continental shelf and submarine canyons (Freiwald *et al.*, 2004).

Submarine canyons incise many continental slopes around the world (Harris and Whiteway, 2011) and are considered to have an important ecological role (Fernandez-Arcaya *et al.*, 2017: Annex I). The complex topography of canyons creates specific hydrological and sedimentation regimes exposing hard substrate (De Leo *et al.*, 2010). The interplay of hydrodynamics, e.g. strong bottom and tidal currents, and sedimentation rates creates high substrate heterogeneity in submarine canyons, including areas of erosion and areas of sediment deposition. Canyons also enhance the mixing of water masses, especially in the canyon head, and the nutrients released in the surface waters increase plankton growth (Huthnance, 1995). This primary production is transported into the submarine canyons as they act as conduit for the transportation of organic matter (Amaro *et al.*, 2015; Amaro *et al.*, 2016; De Leo *et al.*, 2010). Due to the topography, the specific patterns in hydrology, hydrodynamics and sedimentation, and the relative high food supply, canyons favour the presence of cold-water corals and the formation of habitats constructed by these type of organisms (e.g. De Leo *et al.*, 2010; Mortensen and Buhl-Mortensen, 2005).

The continental slope of the Bay of Biscay is dominated by submarine canyons. Cold-water corals are known to exist in this basin since the late 19th century, but the knowledge about their distribution was very limited. The first report on these cold-water corals was to warn for these “pests for trawlers” (Joubin, 1922). Since then, only few studies have investigated the distribution of cold-water corals within the study area of interest (De Mol *et al.*, 2011; Le Danois, 1948; Reveillaud *et al.*, 2008; Zibrowius, 1980). The presence of fisheries and marine litter is also reported in the Bay of Biscay (e.g. Berthou *et al.*, 2014; Galgani *et al.*, 2000; Joubin, 1922; Pham *et al.*, 2014). However, marine management plans are rare in the Bay of Biscay and do not concern benthic habitats. The lack of knowledge of the distribution of cold-water coral habitats in the Bay of Biscay limits the development of a conservation strategy. It is, thus, necessary to understand the distribution of cold-water coral habitats within this basin, before any protection measures can be set in place.

3. The project CoralFISH and data collection

Developing conservation tools was one of the goals set in the European project CoralFISH (FP7-funded; grant agreement no. 213144) that ran from 2008 to 2012. This project assessed the interaction between cold-water corals, fish and the fishing industry in order to develop tools for monitoring and predictive models for ecosystem based management in European waters and beyond (<http://eu-fp7-coralfish.net/>). Among the objectives was the evaluation of the distribution of deep-water bottom fishing effort to identify areas of interaction between fishing gear and cold-water coral ecosystems and the impact on these habitats as well as the development of essential methodologies and indicators for baseline and subsequent monitoring of closed areas.

Due to the limited knowledge about the distribution of corals in the Bay of Biscay, collecting new data was important to be able to provide information about this distribution. Three large cruises (BobGeo, BobGeo 2 and BobEco) were part of the CoralFISH project and collected data on cold-water coral habitats, especially the reef-forming scleractinians *L. pertusa* and *M. oculata*, using a towed camera (BobGeo) or a Remotely Operated Vehicle (ROV; BobEco). Additional data was opportunistically collected by the towed camera during four additional cruises (Evhoe). I have participated in an ROV cruise (BobEco) and one of the Evhoe cruises (Evhoe 2013). A total of 24 canyons were explored during 46 dives to investigate the distribution and ecology of cold-water coral habitats and their communities and comprised a large spatial extent (Fig. 1).

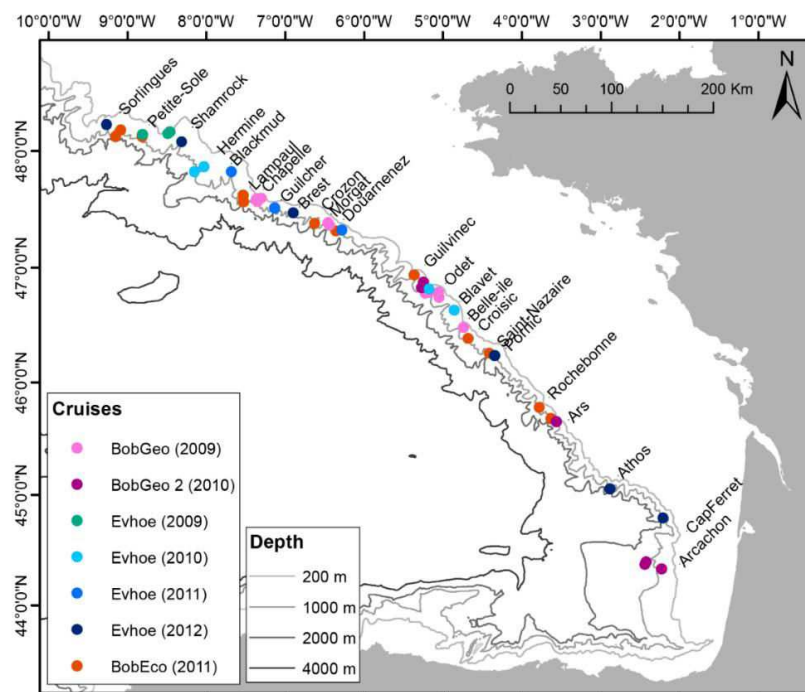


Figure 1: The cruises analysed in this study. Each colour represents one cruise and each dot is one dive. Data were acquired with an ROV on the BobEco cruise and with a towed camera on the other cruises. The names of the explored canyons are shown. ‘La Chapelle Canyon’ is not the official name of the canyon north of the Éperon Ostrea. However, for practical reasons, we will refer to this unnamed canyon as La Chapelle, after the sandbanks on the continental shelf above this canyon.

A coral biota classification system was developed within the CoralFISH project, including 15 biotopes or habitats described by the dominant coral(s) and substrate type (Davies *et al.*, 2017: Annex II). This classification was used in the present work to analyse the image footage acquired by the ROV and towed camera by establishing cold-water coral habitats on each image.

4. Thesis objectives

This thesis aimed at improving the knowledge and understanding of the distribution, diversity and functions of cold-water coral habitats in the Bay of Biscay, with the overarching goal of providing a sound scientific basis for the development of strategies for preservation of these vulnerable habitats. In more detail, four main objectives were established:

1. To describe the heterogeneity and diversity of cold-water coral habitats associated with submarine canyons in the Bay of Biscay.
2. To determine the factors influencing the distribution of cold-water coral habitats at different spatial scales.
3. To investigate the diversity and composition of the megafaunal communities associated with the cold-water coral habitats and to identify the abiotic and biotic factors influencing this diversity and composition.
4. To identify potential impacts of human activities on cold-water coral habitats in the form of marine litter, including fishing gear.

The **first chapter** gives an overview of the characteristics of submarine canyons and cold-water corals.

The **second chapter** describes the geological and oceanographic contexts of the Bay of Biscay, with a focus on those factors that may promote the development of cold-water coral habitats.

The **third chapter** is a paper published in *Frontiers in Marine Science* (Van den Beld *et al.*, 2017). It addresses the two first objectives of this study. The distribution of cold-water coral habitats and the composition of coral assemblages in the submarine canyons of the Bay of Biscay are described. Abiotic drivers of the distribution of the habitats are sought among geographic, geomorphologic and oceanographic factors. Main research questions were: (1) What are the nature and the diversity of cold-water coral habitats, and (2) What is the spatial distribution, at regional and local scales, of these cold-water coral habitats. We have hypothesised that the distribution is constrained by the hydrodynamic regime and the sedimentation patterns on both a regional (Bay of Biscay) and a local (canyon) scale. Substrate type, a result of the interplay of hydrodynamics and sedimentation, is an important factor controlling the coral habitat distribution. To be more specific, the northwestern flank of canyons, exposed to the dominant current, favours the development of cold-water corals. Further, we have explored if we could confirm the observations of De Mol *et al.* (2011) that

observed live coral reefs deeper than 350 m water depth and coral rubble at water depths shallower than 350 m.

The **fourth chapter** is a manuscript in preparation that describes the megafaunal community associated with cold-water coral habitats and responds to the third objective. Abundances and diversity of the non-coral species associated with the different coral habitats are given. The species composition is also described. Further, the influences of abiotic factors, such as dominant substrate type, as well as biotic factors, such as coral density or coverage, are investigated. The main questions are: (1) Do the cold-water coral habitats, defined *a priori* by their dominant species and substrate, differ in the structure and composition of the associated fauna? and (2) Are coral reefs characterised by a higher diversity (i.e. 'biodiversity hotspots') than other cold-water coral habitats?

The **fifth chapter** (Van den Beld *et al.*, 2016) describes the distribution of litter in the submarine canyons of the Bay of Biscay. This chapter responds to the fourth objective of this thesis. The chapter gives a description of litter observed on image footage in submarine canyons of the Bay of Biscay, including their distribution across the basin and across depths. Further, the influence of seafloor relief on the distributions is given as a measure of potential impact on biological structures, e.g. corals, emerging from the seafloor. It also discusses the potential origin of the litter items and their potential impact on corals.

A general conclusion summarises the main results of this thesis, and is followed by the perspectives, including:

1. Recommendations for sampling effort and strategy to complete our knowledge about cold-water corals in the Bay of Biscay.
2. The inputs, limitations and short-term perspectives of habitat suitability models using the existing dataset.
3. The implication of this thesis in the conservation and the direct applications to which it has contributed in terms of a proposal for major Natura 2000 sectors.

Three scientific papers with a contribution as co-author are presented as annexes:

Annex I. review on the ecological role of canyons by Fernandez-Arcaya *et al.* This paper is **published** in the special issue *Horizon Scan 2017: Emerging Issues in Marine Science* of the scientific journal *Frontiers in Marine Science* (Fernandez-Arcaya *et al.*, 2017).

Annex II. paper about the classification system developed during the CoralFISH project by Davies *et al.* This paper is **in press** in the special issue CoralFISH that will appear in the scientific journal *Deep-Sea Research II* and is available online (Davies *et al.*, 2017).

Annex III. paper that reports on the co-occurrences of *L. pertusa* and *M. oculata* in the submarine canyons of the Bay of Biscay par Arnaud-Haond *et al.* This paper is **in press** in the special issue CoralFISH that will appear in the scientific journal *Deep-Sea Research II* and is available online (Arnaud-Haond *et al.*, 2015).

This manuscript is bilingual. The introduction and the general conclusions and perspectives are both in English and in French. The chapters are written in English, but will begin with a summary of the chapter in French.

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Chapter 1

Submarine canyons and cold-water corals at stake

Résumé français

Les canyons sous-marins et les coraux d'eau froide : des écosystèmes à enjeux

1. Les canyons sous-marins

Les marges continentales ont une hétérogénéité d'habitat élevée qui influence la diversité à plusieurs échelles, depuis celle des conditions hydrographiques, et celle des structures géologiques ou physiographiques telles que les canyons sous-marins, à celle des habitats biogéniques formés par les organismes structurants, comme les coraux d'eau froide (Levin et Sibuet, 2012 ; Menot *et al.*, 2010). Les canyons sous-marins sont des vallées avec des flancs accidentés qui incisent les plateaux et pentes de nombreuses marges continentales de l'océan mondial (Harris *et al.*, 2014 ; Harris et Whiteway, 2011). Les canyons forment la connexion entre le plateau continental et la plaine abyssale et sont considérés comme des conduits privilégiés pour le transport de sédiment (De Stigter *et al.*, 2007), ainsi que des puits de matière organique et de carbone (par ex. Masson *et al.*, 2010 ; Van Oevelen *et al.*, 2011).

Les canyons sous-marins tirent leur origine de plusieurs événements, dont l'érosion de la pente par des éboulements et glissements sédimentaires, et des courants de turbidité sont les plus importants (Shepard, 1981 ; Shepard *et al.*, 1979). Trois types de canyons sous-marins peuvent être distingués (Harris et Whiteway, 2011) : (1) les canyons qui incisent un plateau continental et qui ont une tête de canyon clairement connectée à une rivière majeure, (2) les canyons qui incisent un plateau continental, sans connexion claire avec une rivière, mais qui ont été formés par des courants d'érosion et (3) les canyons « aveugles » qui incisent la pente continentale, sans connexion avec une rivière, et créés par des éboulements ou des ruptures de pente (Harris et Whiteway, 2011).

La topographie hétérogène, complexe et accidentée des canyons sous-marins a une influence sur les courants en créant des accélérations de courants, des ondes internes et des cascades d'eau plus dense provenant du plateau (Allen et Durrieu de Madron, 2009 ; De Leo *et al.*, 2010 ; Harris et Whiteway, 2011). Le régime hydrodynamique inclut également les courants de marée, et les courants de turbidité pour les canyons connectés à une rivière (par ex. Shepard *et al.*, 1974 ; Amaro *et al.*, 2016 ; Canals *et al.*, 2006 ; Arzola *et al.*, 2008). Les processus d'érosion et de sédimentation dans les canyons sous-marins sont liés à l'hydrodynamisme ; le sédiment est soit érodé et/ou transporté plus loin dans les canyons soit déposé sur le fond, selon le régime de courants.

Les processus hydrodynamiques sont également importants pour la production et le transport du carbone organique dans les canyons (par ex. De Leo *et al.*, 2010 ; Huthnance, 1995). La production primaire est augmentée au niveau des canyons par des phénomènes d'*upwelling*,

particulièrement causé par des ondes internes. Des substances nutritives deviennent ainsi accessibles au plancton (par ex. Huthnance, 1995) induisant une efflorescence phytoplanctonique. Les phénomènes de *downwelling* à l'inverse participent au transport de la matière organique de la tête vers le bas du canyon.

La topographie complexe, un régime spécifique d'hydrodynamisme, des patrons de sédimentation qui exposent parfois le substrat dur ou parfois déposent le sédiment, les apports trophiques propres et les interactions entre ces processus sont caractéristiques des canyons sous-marins et favorisent le développement des habitats de coraux d'eau froide.

2. Les coraux d'eau froide

Les coraux d'eau froide sont définis par Cairns (2007) comme étant des cnidaires pourvus d'un squelette calcaire ou protéique. Selon cette définition, les ordres taxonomiques Scleractinia, Antipatharia, Alcyonacea et Pennatulacea et les familles taxonomiques de Stylasteridae et Milleporidae sont des coraux d'eau froide ainsi que quelques espèces de Zoanthidea et d'Hydractiniidae (Cairns, 2007).

Plus de 5000 espèces de coraux d'eau froide sont connues, la majorité d'entre elles sont des espèces profondes, vivant à des profondeurs supérieures à 50 m et dépourvues de zooxanthelles (Cairns, 2007).

2.1. Les scléractiniaires

Les scléractiniaires ont un exosquelette calcaire. Environ 40% des espèces de scléractiniaires sont considérées comme des espèces d'eau profonde, dont environ trois-quarts sont solitaires, alors que les autres sont coloniaux (Cairns, 2001 ; Cairns, 2007). Les scléractiniaires sont généralement considérés comme des filtreurs s'alimentant de phytoplancton et de matière organique dissoute (Roberts *et al.*, 2009). Des études récentes indiquent que les scléractiniaires *Lophelia pertusa* et *Madrepora oculata* se nourrissent de matière en suspension « fraîche » (Duineveld *et al.*, 2007), de matière organique dissoute (Mueller *et al.*, 2014), de phytodétritus (Duineveld *et al.*, 2007), de phytoplancton (Carlier *et al.*, 2009) et de zooplancton (Carlier *et al.*, 2009 ; Duineveld *et al.*, 2004 ; Hebbeln *et al.*, 2014 ; Mienis *et al.*, 2012). Les scléractiniaires ont des longévités élevées et des taux de croissance faibles ; par exemple *L. pertusa* et *M. oculata* ont des taux de croissance estimés à environ 2 à 26 mm par an, basés sur des expériences dans un aquarium et des colonies sur plate-forme pétrolière (Bell et Smith, 1999 ; Gass et Roberts, 2006 ; Orejas *et al.*, 2008). Les scléractiniaires profonds sont gonochoriques ; les colonies mâles et femelles sont séparées (e.g. Brooke and Young, 2003 ; Waller and Tyler, 2005 ; Waller *et al.*, 2002 ; 2008). La reproduction est peu connue, mais les scléractiniaires se reproduisent asexuellement, par bourgeonnement ou fragmentation (e.g. Harrison, 2011 ; Highsmith, 1982), et sexuellement, où la fécondation est probablement externe (e.g. Brooke and Young, 2003 ; Roberts *et al.*, 2009 ; Waller *et al.*, 2002). La reproduction sexuelle pourrait avoir des variations saisonnières, lié à l'augmentation de température et/ou l'occurrence des floraisons planctoniques (Brooke and Järnegren, 2013).

Des scléactiniaires ont été observés dans tous les océans, à l'exception de la mer de Béring et la plupart de l'Arctique (Cairns, 2007 ; Roberts *et al.*, 2006). Parmi les scléactiniaires d'eau profonde, les scléactiniaires récifaux *L. pertusa* et *M. oculata* sont les plus connus et les mieux étudiés, en particulier dans l'Atlantique du Nord-Est ; ce biais d'exploration fausse la distribution de ces espèces et des scléactiniaires récifaux en général (Cairns, 2007 ; Roberts *et al.*, 2006). Des scléactiniaires ont été observés sur la marge continentale, associés à une variété d'entités géomorphologiques tels que canyons sous-marins, fjords et le rebord du plateau continental (par ex. Freiwald *et al.*, 2004 ; Mortensen *et al.*, 2001).

Des scléactiniaires ont été observés à toutes les profondeurs et peuvent atteindre au moins 4800 m dans l'Atlantique Nord-Est (Zibrowius, 1980). Les espèces récifales, surtout *L. pertusa* et *M. oculata*, se trouvent habituellement entre 50 et 1000 m de profondeur (Roberts *et al.*, 2006). Les récifs de *L. pertusa* se trouvent dans des eaux avec une température entre 2 et 13°C (Freiwald *et al.*, 2004 ; Roberts *et al.*, 2006). Quelques espèces de scléactiniaires, par exemple *M. oculata*, peuvent supporter des températures de 15°C en Méditerranée (Zibrowius, 1980). Des scléactiniaires récifaux ont été observés dans des eaux avec une salinité entre 32 et 38 pss (Davies et Guinotte, 2011 ; Davies *et al.*, 2008 ; Freiwald *et al.*, 2004) et dans une enveloppe de densité spécifique de 27,35 à 27,65 kg m⁻³ pour les récifs de *L. pertusa* dans l'Atlantique Nord (Dullo *et al.*, 2008). Cette enveloppe pourrait différer entre régions, car les colonies vivantes de *L. pertusa* ont été trouvées à des densités de 27,1-27,2 kg m⁻³ dans le Golfe du Mexique (Davies *et al.*, 2010), à des densités de 27,62-27,71 kg m⁻³ au large de Groenland (Kenchington *et al.*, 2017), et des densités de 28,80-29,35 kg/m³ en Méditerranée (Flögel *et al.*, 2014 ; Freiwald *et al.*, 2009 ; Gori *et al.*, 2013 ; Lo Iacono *et al.*, 2014 ; Taviani *et al.*, 2015). La concentration en carbonate de calcium dans l'eau de mer est un facteur contraignant les occurrences et la distribution des scléactiniaires, parce que les scléactiniaires précipitent le carbonate de calcium, requis pour leur squelette (Cairns, 2007).

L. pertusa et *M. oculata* ont été observés dans des zones avec des régimes hydrodynamiques turbulents (par ex. Mortensen *et al.*, 2001 ; Roberts *et al.*, 2009), favorables à leur approvisionnement alimentaire avec, par exemple, les ondes internes et *downwelling* (Davies *et al.*, 2009 ; Frederiksen *et al.*, 1992). A l'échelle régionale, le régime hydrodynamique et la circulation générale des courants sont importants également pour la dispersion larvaire et la connectivité entre populations. Quelques études qui ont abordées le sujet ont montré que la dispersion larvaire était limitée pour les scléactiniaires, incluant 15 espèces de 9 familles (Le Goff-Vitry *et al.* 2004), dont *L. pertusa* (Dahl *et al.*, 2012 ; Le Goff-Vitry *et al.* 2004 ; Morrison *et al.*, 2011). Il existe un échange de gène restreint, avec un recrutement local, entre les populations de la marge Ibérique jusqu'aux fjords de Scandinavie (Le Goff-Vitry *et al.* 2004) et entre l'Atlantique Nord-Est et du Nord-Ouest, incluant le Golfe de Mexique, la côte des États-Unis, et trois régions du Royaume-Uni et de Norvège (Morrison *et al.*, 2011).

Les récifs de coraux d'eau froide supportent une biodiversité élevée (Freiwald *et al.*, 2004 ; Roberts *et al.*, 2009) et une biomasse élevée (Van Oevelen *et al.*, 2009). La diversité élevée des récifs de *L. pertusa* est probablement augmentée par une forte hétérogénéité formée par la structure tridimensionnelle des colonies (Buhl-Mortensen *et al.*, 2010 ; Mortensen *et al.*, 1995).

Par conséquent, les récifs sont supposés fournir des refuges et fonctionnent comme des zones d'alimentation et nurseries pour un nombre d'organismes, incluant les poissons et crustacés d'importance commerciale (par ex. Freiwald *et al.*, 2004 ; Roberts *et al.*, 2006).

2.2. Les antipathaires, gorgones et pennatules

Les agrégations formées par des antipathaires, des gorgones et/ou pennatules, souvent appelés des jardins ou forêts de coraux, auraient des fonctions similaires à celles des récifs de scléactiniaires (Freiwald *et al.*, 2004). Il y a environ 235 d'espèces d'antipathaires (Cairns, 2007 ; Daly *et al.*, 2007), 200 d'espèces de pennatules (Williams, 1995 ; Williams, 2011) et plus de 2700 espèces de coraux mous (alcyonaires), dont environ 1300 espèces de gorgones (Daly *et al.*, 2007 ; Watling *et al.*, 2011). Approximativement, 75% des antipathaires et 75% des octocoralliaires, incluant les gorgones et pennatules, sont considérés comme des coraux d'eau profonde, car vivant au-delà de 50 m de profondeur (Cairns, 2007). La majorité des antipathaires et des gorgones ont besoin de substrat dur pour s'installer, tandis que les pennatules s'installent sur du substrat meuble (par ex. Roberts *et al.*, 2009 ; Wagner *et al.*, 2012a ; Williams, 2011). Le régime alimentaire des coraux non-scléactiniaires n'est pas complètement connu, mais plusieurs études ont montré que certaines gorgones se nourrissent de phyto- et zooplancton (Carlier *et al.*, 2009). Le régime alimentaire de l'antipathaire *Leiopathes glaberrima* inclut du zooplancton également, mais la proportion de zooplancton au régime alimentaire est plus faible que chez les scléactiniaires *L. pertusa*, *M. oculata*, *Desmophyllum dianthus* et la gorgone *Paramuricea* cf. *macrospina* (Carlier *et al.*, 2009). Ces coraux d'eau froide ont également une longévité élevée et des taux de croissance faibles (par ex. Bo *et al.*, 2015 ; De Moura Neves *et al.*, 2015b ; Sherwood et Edinger, 2009 ; Wagner *et al.*, 2012a). Comme les scléactiniaires, la plupart des espèces d'antipathaires, de gorgones et de pennatules profonds sont gonochoriques (Kahng *et al.*, 2011 ; Wagner *et al.*, 2012b). Ils se reproduisent asexuellement par bourgeonnement ou fragmentation et sexuellement, probablement par fécondation externe (e.g. Beazley and Kenchington, 2012 ; Edwards and Moore, 2008 ; Watling *et al.*, 2011). Chez certaines espèces les embryons sont « maternels » par la colonie adulte (Orejas *et al.*, 2007). La reproduction pourrait être saisonnière, lié à l'augmentation de température d'eau et les floraisons planctoniques.

La distribution des antipathaires et des octocoralliaires est étendue ; ils sont observés dans tous les océans des tropiques jusqu'à l'Arctique (Wagner *et al.*, 2012a ; Watling *et al.*, 2011 ; Williams, 1995). Ces coraux non-scléactiniaires sont également observés à toutes les profondeurs ; des pennatules sont observés du plateau jusqu'à au moins de 6000 m de profondeur (Williams, 1995 ; Williams, 2011), des antipathaires sont observés jusqu'à 8600 m (voir Wagner *et al.*, 2012a) et des gorgones jusqu'à 8000 m, même si la plupart se trouvent au-dessus de 2000 m (Yesson *et al.*, 2012). Les conditions environnementales des antipathaires, gorgones et pennatules sont moins connues que celles des scléactiniaires, parce que la majorité des études se focalisent sur des scléactiniaires récifaux. Cependant, des antipathaires et octocoralliaires ont été observés dans des eaux avec une température de 0 à 10°C (Yesson *et al.*, 2015) et 5 à 11°C (Yesson *et al.*, 2012), respectivement. L'hydrodynamisme est aussi important pour les antipathaires, gorgones et pennatules que pour les scléactiniaires, puisqu'ils

sont également dépendants d’approvisionnement nutritif par les courants. La dispersion larvaire est très peu connue, mais pourrait être très limitée. Dans l’Atlantique Nord-Ouest, un modèle de dispersion larvaire basé sur les conditions hydrodynamiques locales prédit que deux populations de l’antipathaire *L. glaberrima* séparées par un canyon ne sont pas connectées (Cardona *et al.*, 2016). La connectivité basse entre les populations d’antipathaires *Antipathes fiordensis* en Nouvelle Zélande suggère également une dispersion larvaire locale (Miller, 1997 ; Miller, 1998).

Des coraux non-scléractiniaires pourraient créer une hétérogénéité d’habitat, particulièrement dans les zones où le relief est par ailleurs faible (Buhl-Mortensen *et al.*, 2010 ; Tissot *et al.*, 2006). Cette hétérogénéité d’habitat pourrait augmenter la densité et diversité de la faune associée mais ceci reste une hypothèse (Hargrave *et al.*, 2004 ; Henry et Roberts, 2007 ; Robert *et al.*, 2014). Les jardins de coraux construits par ces coraux ont été observés être utilisés comme des refuges, des zones d’alimentation et de reproduction par d’autres organismes (par ex. Baillon *et al.*, 2012 ; Buhl-Mortensen *et al.*, 2010 ; Le Guilloux *et al.*, 2010).

3. L’impact anthropique

L’océan profond est soumis à des pressions anthropiques croissantes à cause d’un épuisement des ressources terrestres et côtières (Ramirez-Llodra *et al.*, 2011). Cependant, chaque type d’activité humaine, que ce soit les forages de pétrole ou de gaz, la pêche ou le tourisme, laisse une empreinte sur les écosystèmes marins. L’impact des déchets, de la pêche et du changement climatique sont probablement des menaces importantes pour les coraux d’eau froide.

3.1. Les déchets

Une description de la distribution des déchets marins est nécessaire pour aider à établir les stratégies de gestion, comme la Directive Cadre Stratégie pour le Milieu Marin (DCSMM). De nombreux objets pourraient être considérés comme des déchets, dont les plastiques sont les plus abondants (par ex. Galgani *et al.*, 2015 ; Pham *et al.*, 2014b ; Ramirez-Llodra *et al.*, 2013). Le fond marin est un grand puits pour des déchets (Galgani, 2015 ; Galgani *et al.*, 1995). L’hydrodynamisme contrôle la circulation, la distribution et l’accumulation des déchets (Galgani *et al.*, 2000 ; Mordecai *et al.*, 2011 ; Pham *et al.*, 2014b) et pourrait amener les déchets aux zones les plus profondes et les plus isolées des océans.

Plus spécifiquement, les canyons sous-marins sont des conduits pour des déchets qui sont transportés du plateau continental jusqu’à l’environnement profond (par ex. Galgani *et al.*, 1996 ; Pham *et al.*, 2014b ; Ramirez-Llodra *et al.*, 2011), tout comme les sédiments. La densité de déchets est en effet plus élevée dans les canyons sous-marins que sur d’autres entités géomorphologiques, comme les plateaux continentaux ou les monts sous-marins (Pham *et al.*, 2014b) et peuvent dépasser le millier d’objets par km² (par ex. Pham *et al.*, 2014b ; Ramirez-Llodra *et al.*, 2013). La rugosité du fond marin, créé par des éléments biologiques ou géologiques, par exemple des coraux ou des affleurements rocheux, peut concentrer et conserver des déchets (Galgani *et al.*, 2015 ; Schlining *et al.*, 2013). En effet, les déchets sont

plus abondants dans certaines zones rugueuses, à cause de la présence des affleurements rocheux ou des éponges (Bergmann et Klages, 2012 ; Schlining *et al.*, 2013).

Les déchets ont une origine terrestre ou maritime, même si cette origine est parfois difficile à distinguer. Les plastiques, par exemple, peuvent être transportés depuis la terre par des rivières, mais peuvent également tirer leur origine des bateaux. Une origine maritime est plus probable pour les déchets plus lourds, comme les bouteilles en verre, parce que ces objets coulent plus rapidement.

L'étouffement, l'enchevêtrement ou ingestion des déchets pourraient causer la mort ou la nécrose des colonies de coraux d'eau froide (revue par Kühn *et al.*, 2015). Des déchets pourraient impacter la faune dans les sédiments également en induisant des phénomènes d'anoxie (Kühn *et al.*, 2015 ; Mordecai *et al.*, 2011). Cependant, des déchets peuvent être colonisés par de la faune et potentiellement augmenter la biodiversité locale.

La distribution des déchets reste compliquée à estimer, avec plus de 95% de l'environnement profond inexploré. L'extension exacte de l'impact des déchets est encore donc largement inconnue, mais aussi leur impact à l'échelle des populations, colonies et organismes, comme celles des coraux d'eau froide (Kühn *et al.*, 2015).

3.2. La pêche

Après les années soixante, l'effort de pêche s'est déplacé vers les eaux plus profondes, à cause de l'épuisement des ressources halieutiques côtières, des régulations de la pêche côtière et de l'amélioration des techniques de pêche (Ramirez-Llodra *et al.*, 2011). Les chaluts de fond sont probablement la menace la plus élevée pour les coraux d'eau froide (Benn *et al.*, 2010). La concentration de bancs de certaines espèces de poissons, comme l'hoplostèthe orange, autour des récifs de coraux et dans les canyons sous-marins (Koslow *et al.*, 2007 ; Lorance *et al.*, 2002 ; Uiblein *et al.*, 2003), augmentent l'effort de pêche en bordure ou dans ces habitats. La pêche au chalut peut endommager sérieusement les récifs de coraux. Fosså *et al.* (2002) ont estimé que 30 à 50% des récifs norvégiens de *L. pertusa* ont été endommagés par le chalutage. Des communautés de coraux d'eau froide pourraient être impactées par les effets directs de la pêche (revu par Clark *et al.*, 2016) par (i) destruction des espèces structurantes, (ii) diminution de leur abondance et biomasse, (iii) changements dans les compositions d'espèces, et (iv) réduction de la diversité, mais aussi par des effets indirects comme (v) l'augmentation des dépôts de sédiment re-suspendu par le chalutage (Martín *et al.*, 2014a ; Palanques *et al.*, 2006), (vi) des changements du relief du fond sous-marin, en particulier les flancs de canyons qui deviennent plus lisses (Puig *et al.*, 2012), et (vii) des changements de substrat, réduisant l'hétérogénéité de celui-ci (Martín *et al.*, 2014a ; Mengual *et al.*, 2016).

La récupération des communautés de coraux d'eau froide est un processus qui nécessite un temps long. Certaines études ont observé que les communautés chalutées ne sont pas arrivées à leur état d'avant chalutage après au moins 5 ans (Williams *et al.*, 2010), 8 ans (Huvenne *et al.*, 2016) ou 10 ans (Williams *et al.*, 2010), même pas après 38 ans (Baco, 2016). Ce n'est pas surprenant, au vu des faibles taux de croissance estimés pour les coraux d'eau froide qui constituaient ces récifs.

Les coraux d'eau froide pourraient également être impactés par les palangres de pêche, même si dans une moindre mesure que la pêche au chalut (Fabri *et al.*, 2014 ; Fosså *et al.*, 2002 ; Pham *et al.*, 2014b). Les impacts principaux des palangres sur des coraux d'eau froide sont l'enchevêtrement et la pêche fantôme par des lignes ou filets de pêche perdus.

3.3. *L'industrie pétrolière*

L'industrie pétrolière pourrait avoir une variété d'impacts sur des coraux d'eau froide, dont la décharge de boues et déblais de forage est probablement la menace la plus forte (Roberts *et al.*, 2009). Ces déchets de forage pourraient étouffer les coraux d'eau froide et d'autres organismes, réduisant l'abondance et la diversité des communautés proche de la source de forage.

Les déversements d'hydrocarbures pourraient avoir des effets sur un plus grande échelle (Ramirez-Llodra *et al.*, 2011). Dans le Golfe du Mexique, les colonies de coraux proches de la source du déversement d'hydrocarbures de Deepwater Horizon en 2010 présentaient d'importantes nécrose jusqu'à 22 km du puits (Fisher *et al.*, 2014).

3.4. *Le changement climatique*

Une autre menace des coraux d'eau froide est liée aux changements globaux qui provoquent un réchauffement et une acidification des océans. L'océan est un puits naturel de dioxyde de carbone, et il a déjà absorbé au moins 30% du CO₂ émis par les activités humaines (IPCC, 2014 ; Ramirez-Llodra *et al.*, 2011), causant une réduction du pH de l'eau de mer (Davies *et al.*, 2007 ; Menot *et al.*, 2010 ; Ramirez-Llodra *et al.*, 2011).

La température de l'eau de mer a augmenté d'environ 0,1°C au cours des quarante dernières années et il est estimé que la température augmenterait encore de 0,5°C dans le prochain siècle (Menot *et al.*, 2010 ; Ramirez-Llodra *et al.*, 2011). Ces augmentations de température pourraient atteindre au moins 700 m de profondeur dans de nombreuses zones de l'océan (Barnett *et al.*, 2005 ; IPCC, 2014) et, par conséquent, pourraient sérieusement impacter des communautés biologiques vivant en environnement profond. Les changements globaux auront également un impact sur les régimes de productivité de surface et de l'approvisionnement en matière organique des fonds marins (Davies *et al.*, 2007 ; Menot *et al.*, 2010) ainsi qu'une modification de l'aire de répartition latitudinale et/ou bathymétrique des espèces (Menot *et al.*, 2010).

Par ailleurs, l'acidification des océans a engendré une augmentation de la concentration du CO₂ de l'eau de mer qui fait descendre le pH par la création d'acide carbonique (H₂CO₃). Par conséquent, les océans deviennent plus acides (Davies *et al.*, 2007 ; Menot *et al.*, 2010). Une conséquence de l'acidification des océans qui impacte particulièrement les coraux d'eau froide, est que les horizons de saturation d'aragonite et de calcite, c'est-à-dire la profondeur à laquelle l'eau de mer devient insaturée par rapport à la concentration d'aragonite ou de calcite, sera située moins profond (Davies *et al.*, 2007 ; Ramirez-Llodra *et al.*, 2011 ; Roberts *et al.*, 2009). Les coraux d'eaux profondes, dont les scléactiniaires récifaux, précipitent le carbonate de calcium sous forme d'aragonite et de calcite à partir de ces éléments présents dans l'eau de mer et, par conséquent, se trouvent habituellement dans des eaux saturées en carbonate de calcium, conditions qu'ils pourraient ne plus rencontrer aux profondeurs auxquelles ils vivent

actuellement (Davies *et al.*, 2007). Même si *L. pertusa* pourrait s'acclimater aux conditions acides, leur squelette sera plus fragile à cause d'un changement dans l'organisation cristalline (Hennige *et al.*, 2015). Un squelette plus fragile casse plus facilement et est plus sensible à l'érosion des animaux comme les éponges.

4. Conservation

Certains habitats coralliens sont des cibles de conservation, du fait de leur longévité, de leur fragilité de leurs rôles fonctionnels importants pour d'autres organismes, et parce qu'ils sont sensibles à l'impact des activités humaines. Plusieurs initiatives internationales, par exemple l'Assemblée Générale des Nations Unies (AG), la convention OSPAR, la Directive Habitats Faune Flore et la Directive Cadre Stratégie pour le Milieu Marin (DCSMM) de la commission européenne et la Convention sur la Diversité Biologique (CDB), ont reconnu l'importance de mettre en place des stratégies de protection des coraux d'eau froide. Ces mesures peuvent prendre plusieurs formes telles que des Aires Marines Protégées (la convention OSPAR notamment), des zones de pêche à accès réglementé ou des règles d'évitement (ORGP) et un réseau de sites de Natura 2000 (Directive Habitats).

Submarine canyons and cold-water corals at stake

1. Submarine canyons

The deep sea is the part of the oceans where photosynthesis cannot take place and is usually defined below 200 meter water depth, including bathyal and abyssal domains. It is an extreme environment with high pressures and no light and is characterised, against first expectations, by a very rich life. The continuous development of new tools in collecting data and creating maps of the seafloor has revealed that continental margins have a high habitat heterogeneity that influences diversity at different scales (Levin and Sibuet, 2012; Menot *et al.*, 2010; Fig. 1). At a large scale, hydrography has an important influence on diversity by the different water masses, productivity, current flows and related substrate types. At a smaller scale of tens of kilometres, the topography of geophysical features creating a specific hydrodynamic regime, e.g. seamounts, banks and submarine canyons, also influence the diversity. At an even smaller scale of several meters to kilometres, habitats formed by engineering species, such as corals and sponges, influence the diversity by providing substrate, shelter and food to organisms. Furthermore, the diversity at this scale is controlled by biotic interactions, e.g. predation and competition.

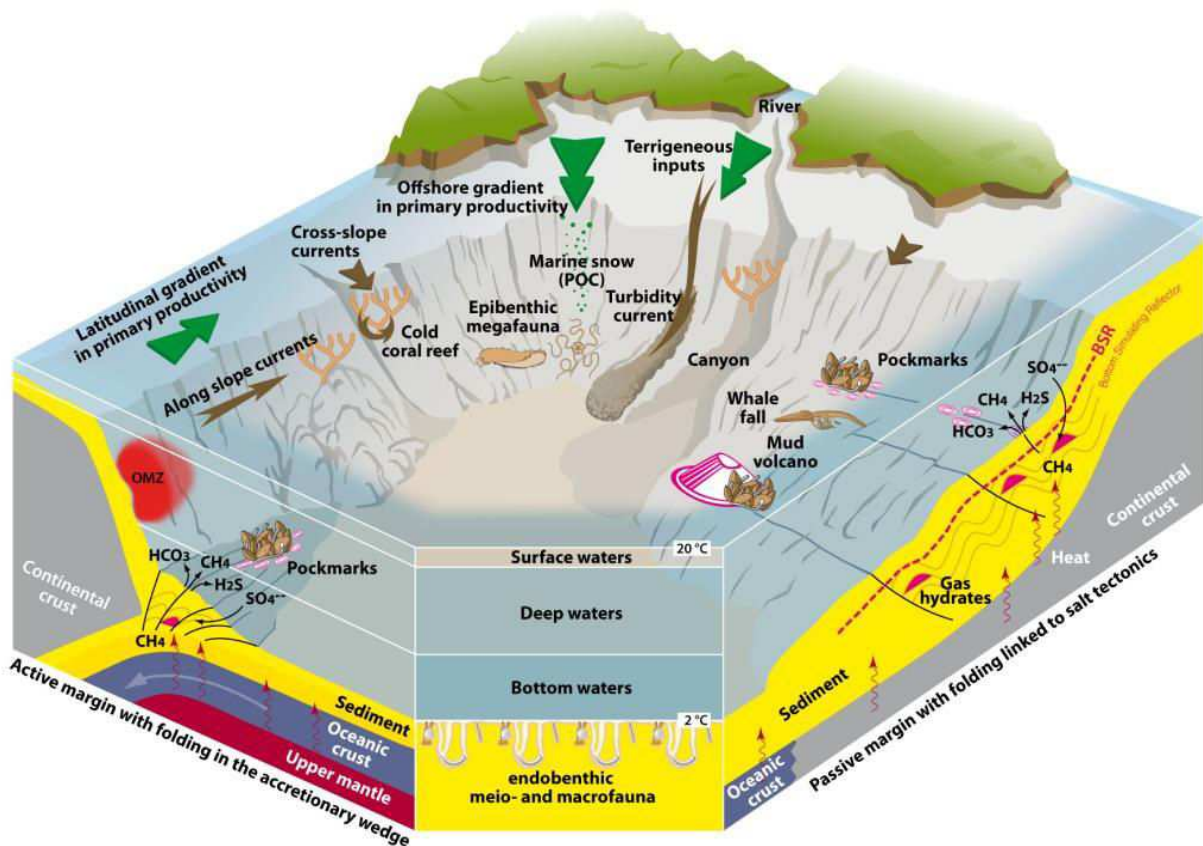


Figure 1: Schematic representation of the main geological, hydrological and biological features on continental margins that influence the biodiversity. Reproduced from Menot *et al.* (2010).

This study focuses on submarine canyons. Submarine canyons are valleys with steep flanks that cut into the shelves and slopes of many continental margins around the world (Harris *et al.*, 2014; Harris and Whiteway, 2011). They are the connection between the continental shelf and the abyss and are considered to be conduits for sediment transport (De Stigter *et al.* 2007) as well as sinks for organic matter and carbon (e.g. Masson *et al.*, 2010; Van Oevelen *et al.*, 2011).

1.1. Morphology

Canyons find their origin in several events, of which erosion of the slope by mass wasting events, e.g. slumping and submarine landslides, and turbidity currents are the most important (Shepard, 1981; Shepard *et al.*, 1979). Canyons evolve further into dendritic complexes by density flow erosion, slumping and by joining smaller adjacent canyons (Harris and Whiteway, 2011). A complex combination of sediment deposition and vertical growth along the canyon flanks and the prevention of deposition along the canyon floor by internal waves and/or turbidity currents create the heterogeneous and complex topography or relief in canyons (Straub and Mohrig, 2009).

The number of canyons in the world has been estimated, but depends largely on the criteria used to define a submarine canyon. Harris and Whiteway (2011) estimated a number of 5849 large submarine canyons worldwide that met criteria as 1000 m depth range span and a width/length ratio of 150:1. Almost 9500 submarine canyons, however, corresponding to 11.2% of the world's continental slope area, were identified by Harris *et al.* (2014) using different criteria.

Canyons can incise active or passive margins and differences between these canyons exist. Active margins are controlled by tectonic/magmatic processes and the widths of the continental shelf and slope of these margins are smaller than passive margins that are controlled by erosion and deposition processes (Fig. 2) (Harris *et al.*, 2014; Harris and Whiteway, 2011).

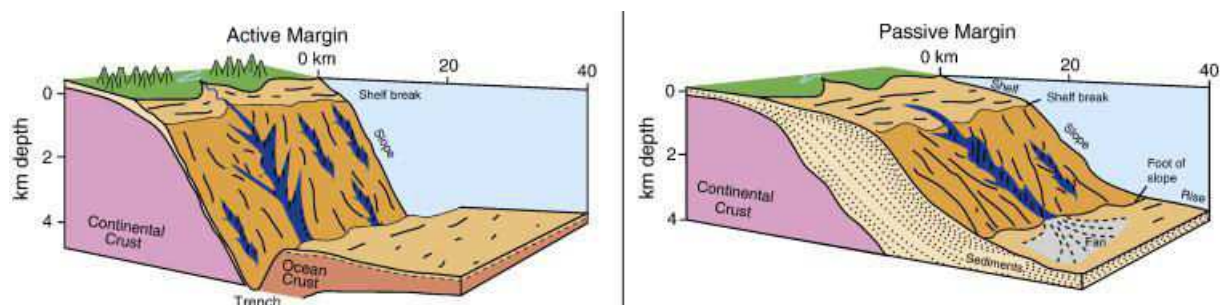


Figure 2: A schematic representation of canyons incising an active margin, characterized by tectonic/magmatic processes and a passive margin, characterized by erosion and deposition processes. Reproduced from Harris and Whiteway (2011).

Harris and Whiteway (2011) probably did the first and largest statistical study of differences in canyons on active and passive margins around the world. The authors identified three types of canyons: (1) canyons that incise a shelf and have a head that is clearly connected to a major river system, and evolve by erosive turbidity flows from fluvial, shelf and upper slope sources, (2) canyons that do incise a shelf, but do not have a clear connection to a river system, but also evolve by erosive currents, and (3) blind canyons incising the continental slope that evolve by

slumping and slope failure processes. Most of the 5849 canyons in their study are type 3 canyons (68.8%) and only a small percentage (2.6%) comprised type 1 canyons. Only the Mediterranean and Black Seas have a larger area of shelf-incising canyons than blind canyons (Harris *et al.*, 2014). Statistical differences were indeed observed between the active margins and passive margins (Harris and Whiteway, 2011). More canyons incised active margins (61.6%) than passive margins (38.4%) and a higher number of canyons were associated to river systems, i.e. type 1 canyons, on active margins. The canyons on these margins were steeper, but canyons on passive margins were more closely spaced, longer in length and the sediment layer in these canyons was thicker. The canyons incising the two different margin types occurred in similar depth ranges (Harris and Whiteway, 2011). These observations are also supported by the study of Harris *et al.* (2014).

1.2. *Hydrodynamics and sedimentation processes*

Due to the presence of a geostrophic flow along continental slopes, exchange between the surface waters and the deep ocean is normally limited (Allen and Durrieu de Madron, 2009). However, the heterogeneous steep and complex topography of submarine canyons has an influence on the currents, since the canyon walls act as a barrier for this dominant along-slope flow, thereby creating accelerated currents, internal waves and dense shelf-water cascading (DSWC) events (Allen and Durrieu de Madron, 2009; De Leo *et al.*, 2010; Harris and Whiteway, 2011). The topography also influences the current directions locally and can cause the current flow to cross the canyon from one side to the other side (Shepard *et al.*, 1974). The sedimentation processes in submarine canyons are narrowly linked with the hydrodynamics, because sediment is either transported further down the canyon or deposited on the seafloor, depending on the current regime. Similarly, erosion of sediment and, therefore, canyons, is also related to currents. The hydrological regime in submarine canyons includes tidal currents, internal waves, dense shelf water cascading and turbidity currents.

Tidal bottom currents in canyons are usually greater than currents higher in the water column (Shepard *et al.*, 1974). Bottom currents can have a down-canyon or up-canyon direction, alternating each other on a semi-diurnal tidal frequency and can be influenced by internal waves within the canyon, as observed in Whittard Canyon in the Bay of Biscay, North-East Atlantic (Amaro *et al.*, 2015; Amaro *et al.*, 2016), in Nazaré Canyon off Portugal, North-East Atlantic (De Stigter *et al.*, 2007) and Monterey Canyon, off California in the Pacific Ocean (Shepard *et al.*, 1974). Usually, these currents have a speed less than 40 cm s^{-1} , what is considered to be moderate to strong (De Stigter *et al.*, 2007; Shepard, 1975; Shepard *et al.*, 1974). Tidal currents are strong enough to transport sediment, e.g. sand, along the canyon axis (De Stigter *et al.*, 2007). Events on the surface of the ocean can influence tidal currents in canyons. Current speeds of both down-canyon and up-canyon directions increased in Carmel and Hueneme Canyons during stormy weather, coinciding with rough seas and strong winds (Shepard *et al.*, 1974).

Another important process in submarine canyons is the presence of **internal waves**. Internal waves are formed because submarine canyons cut the tidal currents that are usually running parallel to the shelf-break topography (Allen and Durrieu de Madron, 2009). Internal waves cause variability in both temperature and salinity (Davies *et al.*, 2010) and will occur in areas

of maximum current speed (Frederiksen *et al.*, 1992). Internal waves have a high energy and can prevent sediment to deposit on the seafloor (Mulder *et al.*, 2012), because the sediment is resuspended in the water column creating intermediate and/or benthic nepheloid layers (Durrieu de Madron *et al.*, 1999; Van Weering *et al.*, 2001). Even though the down-canyon current is dominant in most canyons, internal waves were observed to advance up the canyon or rarely down the canyon in Carmel, Hueneme, Monterey (off California) and Kahaliki (off Hawaii) Canyons in the Pacific Ocean and in Hydrographer (off Georges Bank) and Hudson (off New York) Canyons in the North-West Atlantic (Shepard, 1975; Shepard *et al.*, 1974). Velocities of internal waves can be high but variable between canyons. For example, in Carmel, Monterey and Hueneme Canyons average internal wave velocities were 83, 25 and 50 cm s⁻¹, respectively (Shepard *et al.*, 1974).

Dense shelf-water cascading (DSWC), an event that can cause gravity flows, can also transport large amounts of sediment down submarine canyons (Allen and Durrieu de Madron, 2009; Canals *et al.*, 2006). This process is density-driven and caused by the seasonal cooling of shelf water, especially during winter, that spills over the continental shelf edges and flows along the slope down the canyon (e.g. Canals *et al.*, 2006; Ivanov *et al.*, 2004). Sediment fluxes caused by DSWC can vary between canyons, as it was measured for Cap de Creus and Lacaze-Duthiers Canyons (Mediterranean Sea) in the winter of 2003-2004: the sediment flux in the head of Cap de Creus Canyon was two orders of magnitude stronger than the flux in Lacaze-Duthiers Canyon (Canals *et al.*, 2006). This could be due to differences in the time period the cascading events occurred, which was not simultaneously for all canyons, as well as the difference in duration, ranging from a few hours to several weeks (Palanques *et al.*, 2006a). DSWC could affect the deep sea by increasing sediment loads, current speeds and water density as well as decreasing temperatures. It could be noticed on water depths deeper than 2000 m (Canals *et al.*, 2006; Palanques *et al.*, 2006a; Palanques *et al.*, 2009), but that depends on the intensity of the cascading event; in Cap de Creus Canyon, several cascading events triggered by either storms or river discharges in December 2003, did not reach a water depth of 300 m (Palanques *et al.*, 2009). However, the cascading event in February 2004 was strong enough to increase bottom currents to 80 cm s⁻¹ and the sediment flux to 68 ml l⁻¹ in the same canyon (Palanques *et al.*, 2009). The intensity of cascading events may be related to the width of the continental shelf; events occurring in canyons incising the western Gulf of Lions (Mediterranean Sea) where the shelf is narrower were more intense than in the eastern part of this basin where the continental shelf is larger (Palanques *et al.*, 2006a). Reports of cascading events in canyons of the Bay of Biscay, NE Atlantic, that has a larger shelf than the Gulf of Lions, may be rare; cascading events was reported only once in the relatively well studied Whittard Canyon (Amaro *et al.*, 2016). Furthermore, sediment could be transported a long way in the canyon; in Cap de Creus Canyon, sediment transported by DSWC events was observed approximately 160 km seaward from the head of the canyon (Palanques *et al.*, 2009). Storm-induced downwelling also transports (re)suspended sediment to submarine canyons. Sediment fluxes could be higher when this downwelling coincides with cascading events (Palanques *et al.*, 2006a).

Turbidity currents, causing gravity flows, take also place in canyons and are thought to be one of the processes that created submarine canyons (Shepard, 1981; Shepard *et al.*, 1979). These currents are usually fast moving, intense currents down a slope or canyon that have a high sediment load due to differences in density; the suspended sediment in the water causes

the water density to increase, this water becomes denser than the surrounded water and, thus, moves down the slope. Turbidity currents in canyons could be triggered by river discharges (Arzola *et al.*, 2008), the fast resuspension of river discharge sediment stored on the continental shelf (Palanques *et al.*, 2006a) or by other processes, such as storms (Canals *et al.*, 2006). For example, turbidity currents in Setúbal Canyon, close to the coast of Portugal (NE Atlantic), were fed by the high discharges of the Tagus and Sado Rivers (Arzola *et al.*, 2008). This type of currents could affect a large part of a submarine canyon; it may lose sediment along the way down the canyon, decreasing the sediment flux (Khripounoff *et al.*, 2009). In Var Canyon (Mediterranean Sea), connected to the Var River in France, the sediment flux at 1850 m water depth was approximately 15 to 700 times smaller than the flux at the Var river mouth measured over a period between September 2005 and January 2008 (Khripounoff *et al.*, 2009). The authors suggested that this decrease in sediment flux was due to the variations in settling speeds of large and small particles that settle fast and slow, respectively. At the exception of major rivers still connected to their canyon, e.g. Congo, where a massive and direct transfer of particles driven by strong turbidity currents reaches the deep-sea fan (Savoye *et al.*, 2009), turbidity currents that are strong enough to transport sediment deeper in the canyon do not occur at a regular basis and could happen on a yearly basis or longer timescales, as observed for Nazaré Canyon (De Stigter *et al.*, 2007). Storms are most likely the cause of turbidity currents in Whittard, Audierne and Blackmud Canyons in the Bay of Biscay (Amaro *et al.*, 2016; Mulder *et al.*, 2012).

Canyons are also important locations for **up- and downwelling** of water, where upwelling is usually stronger than downwelling (Allen and Durrieu de Madron, 2009). Upwelling is a flow upwards and flow towards the coast, whereas downwelling is a flow going deeper in the canyon and flows towards the ocean (Allen and Durrieu de Madron, 2009).

Due to the sediment transport and resuspension by the previously described hydrodynamic processes, canyon flanks can be eroded or depositional. In Cap de Creus Canyon, the southern flank was eroded by the DSWC events that mostly occur on this side of the canyon, as observed by the colder temperature and the higher amount of suspended sediment (Fig. 3) (Canals *et al.*, 2006; Puig *et al.*, 2008). Giant furrow fields characterise the southern flank of this canyon indicating that these DSWC events happened repeatedly over time (Canals *et al.*, 2006). Erosion of one canyon flank by the hydrodynamic regime, resulting in the exposure of hard substrate, was also observed in other canyons around the world, including the Mediterranean Sea, the NE and NW Atlantic Ocean (Fabri *et al.*, 2014; Huvenne *et al.*, 2011; Mortensen and Buhl-Mortensen, 2005; Orejas *et al.*, 2009; Sánchez *et al.*, 2014; Van Rooij *et al.*, 2010). The net flow or residual current in the canyons off California, e.g. Monterey Canyon, is downwards, causing the resuspended sediment being transported further down the canyon until it is deposited in the deep-sea fan (Shepard *et al.*, 1974). In Nazaré Canyon, tidal currents were also transporting sediment from the upper to the middle canyon (De Stigter *et al.*, 2007). On the contrary, in Whittard Canyon an up-canyon net-flow was detected, transporting the suspended sediment up the canyon instead of down the canyon (Amaro *et al.*, 2016). The Baltimore Canyon, NW Atlantic, is a submarine canyon with a high sedimentation rate (Hecker *et al.*, 1980). This high input of sediment in this canyon causes a homogenous soft bottom with little rocky outcrops, especially on the canyon walls and the shallower part (Hecker *et al.*, 1980).

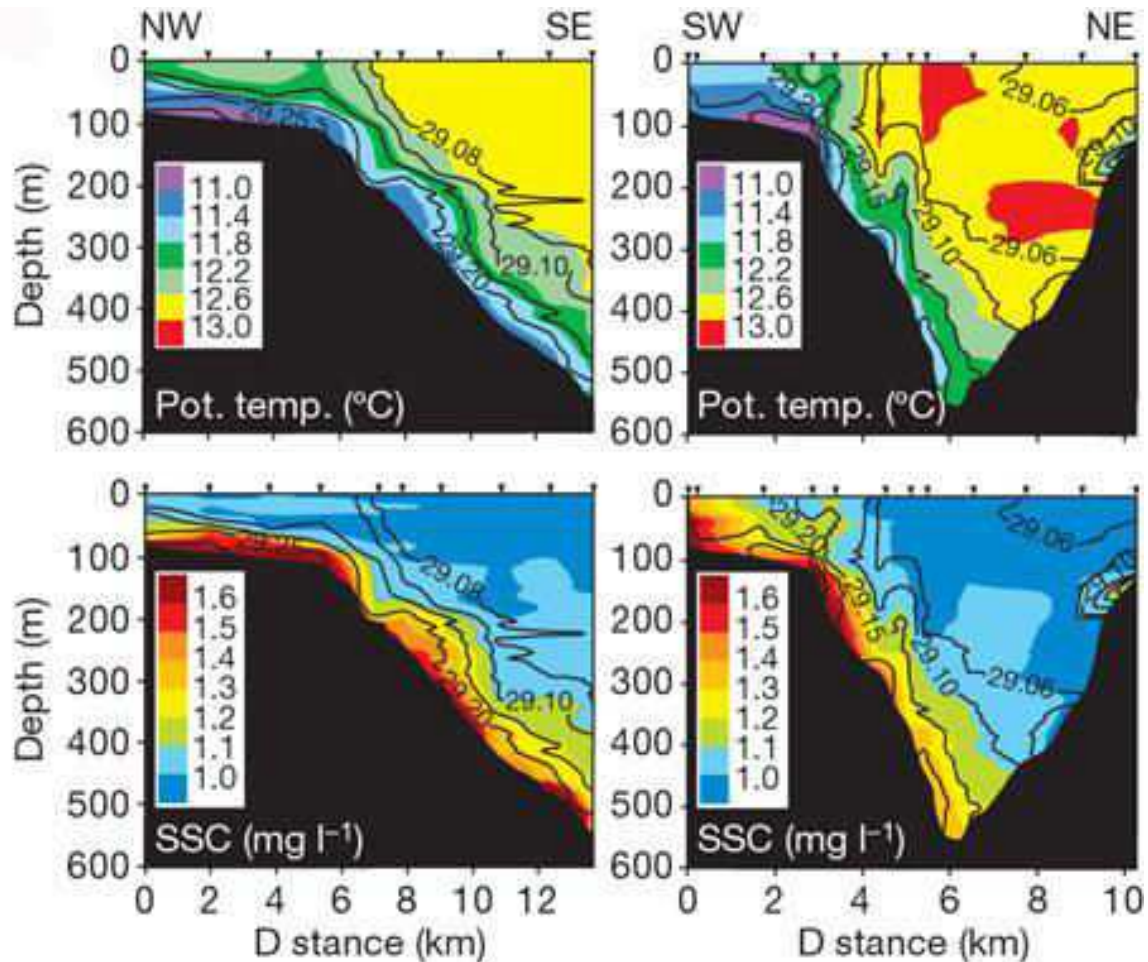


Figure 3: A Dense Shelf-Water Cascading event on 24-26 February 2005 along the southern flank in Cap de Creus Canyon (Mediterranean). The colder potential temperature (top) and the higher suspended sediment concentration (SSC; bottom) indicated a DSWC event starting by cooling shelf water. Reproduced from Canals *et al.* (2006).

1.3. Organic matter

The hydrological processes described above are important in the transport of carbon sources towards deeper parts of the canyons (e.g. Amaro *et al.*, 2015; Amaro *et al.*, 2016; De Leo *et al.*, 2010; Huthnance, 1995). Submarine canyons are, therefore, an important structure for the deep ocean – shelf exchange (Allen and Durrieu de Madron, 2009). Canyons are thought to be a sink for organic carbon and trap it in the sediment. Organic matter reaching submarine canyons can have two origins: (i) derived from primary production and transfer along the food web, and (ii) a continental origin due to the transport of sediment from the shelf and/or sediment resuspension. Therefore, the organic matter reaching the canyon floor, could differ in quality, amount and in time (Etcheber *et al.*, 1999).

Primary production is enhanced by the mixing of water masses, especially caused by internal tides and waves and areas of upwelling. Nutrients are becoming available for plankton, especially at the heads of canyons (Harris and Whiteway, 2011; Huthnance, 1995; Pingree and Mardell, 1985) resulting in planktonic blooms. The primary production is transported in the canyons to deeper water depths by internal tides/waves, bottom currents from the adjacent slope

and downwelling and serves as food for organisms living in the canyon (Amaro *et al.*, 2015; Amaro *et al.*, 2016; Huthnance, 1995). The amount and quality of the food that can be expressed as the suspended particulate organic matter (sPOM) varies between depths. In Whittard canyon, the sPOM was fresher and had a higher proportion of phytoplankton in the upper canyon than in the lower part of the canyon (Amaro *et al.*, 2016). It was suggested that the organic matter arrived in the canyon by lateral transport via bottom currents instead of by gravity flows, as indicated by the amount of phytopigments in the sediment (Amaro *et al.*, 2015). In Cap de Creus Canyon, DSWC events coincided with plankton blooms at the surface, transporting the plankton down canyon (Canals *et al.*, 2006). The resuspension of sediment by tidal currents, internal waves and DSWC could create intermediate and benthic nepheloid layers (Durrieu de Madron *et al.*, 1999; De Stigter *et al.*, 2007; Van Weering *et al.*, 2001); in Nazaré Canyon, there was a close match between semidiurnal increases in current speed and an increase in bottom water turbidity (De Stigter *et al.*, 2007). Nepheloid layers observed in Cap-Ferret and Whittard Canyons (Bay of Biscay) could be 50 to 500 m thick (Durrieu de Madron *et al.*, 1999; Wilson *et al.*, 2015) and had suspended particulate matter (SPM) concentrations between 75 and 300 $\mu\text{g L}^{-1}$ (Wilson *et al.*, 2015). Nepheloid layers occurring in the deeper parts of the canyons could be permanent and less influenced by seasonal variations (De Stigter *et al.*, 2007; Wilson *et al.*, 2015). Nevertheless, seasonal variations were observed in the nepheloid layers between 200 and 1000 m water depth in Cap-Ferret Canyon, with higher turbidity values in early summer than in late spring. These seasonal variations could be related to the primary production in the surface waters (Durrieu de Madron *et al.*, 1999). Likewise, a weak seasonal response of nepheloid layers in the form of increased SPM concentrations has been observed in Whittard Canyon (Wilson *et al.*, 2015).

Carbon burial is controlled by hydrological processes (e.g. Khripounoff *et al.*, 2009). For example, cascading events controlled the carbon input in the form of particulate organic carbon (POC), and generally these events have a higher POC flux than those caused by turbidity currents in the canyons of the Gulf of Lions and Var Canyon (Mediterranean Sea) (Khripounoff *et al.*, 2009). The total organic carbon (TOC) in the sediment was twice as high in the canyons compared to the carbon on the continental slope surrounding the canyon of both Whittard (Duineveld *et al.*, 2001) and Nazaré (Van Oevelen *et al.*, 2011) Canyons. In the latter canyon, carbon burial efficiency was estimated to exceed 30% in high sedimentation areas, even though it was difficult to calculate this due to high reworking of sediment in this canyon (Masson *et al.*, 2010). These results suggest that Whittard and Nazaré Canyons are indeed sinks for carbon. The amount of TOC increased in deeper areas in Whittard Canyon that could be due to gravity flows (Amaro *et al.*, 2015; Amaro *et al.*, 2016). On the contrary, in Nazaré Canyon, the TOC input in the deep parts of the canyon (lower canyon) was approximately one order of magnitude lower than the input in the upper and middle canyon parts (Van Oevelen *et al.*, 2011).

2. Cold-water corals

Cold-water corals (CWCs) are defined as cnidarian species having calcium-carbonate (aragonite or calcite) or black horn-like, proteinaceous skeletal elements (Cairns, 2007). According to this definition, certain anthozoans are considered as cold-water coral: all species of the orders **Scleractinia**, **Antipatharia** (both Hexacorallia), **Alcyonacea** and **Pennatulacea** (both Octocorallia) are CWCs, as well as part of the order **Zoanthidae** and all the species belonging to the hydrozoans families **Stylasteridae** and **Milleporidae** and part of the hydrozoan **Hydractiniidae** family (Cairns, 2007). More than 5000 CWC species are known of which the majority lives below 50 m and are considered as deep-water corals (Cairns, 2007). This limit to distinguish shallow and deep-water corals is chosen by Cairns (2007) because very few zooxanthellate corals live below this depth. The order Alcyonacea includes soft corals that do not have a supporting skeletal axis and gorgonians that do have a supporting skeletal axis (Daly *et al.*, 2007). Examples of colonial scleractinians, a solitary scleractinian, a soft coral (Alcyoniina), a gorgonian, an antipatharian and a pennatulid can be seen in Figure 4.

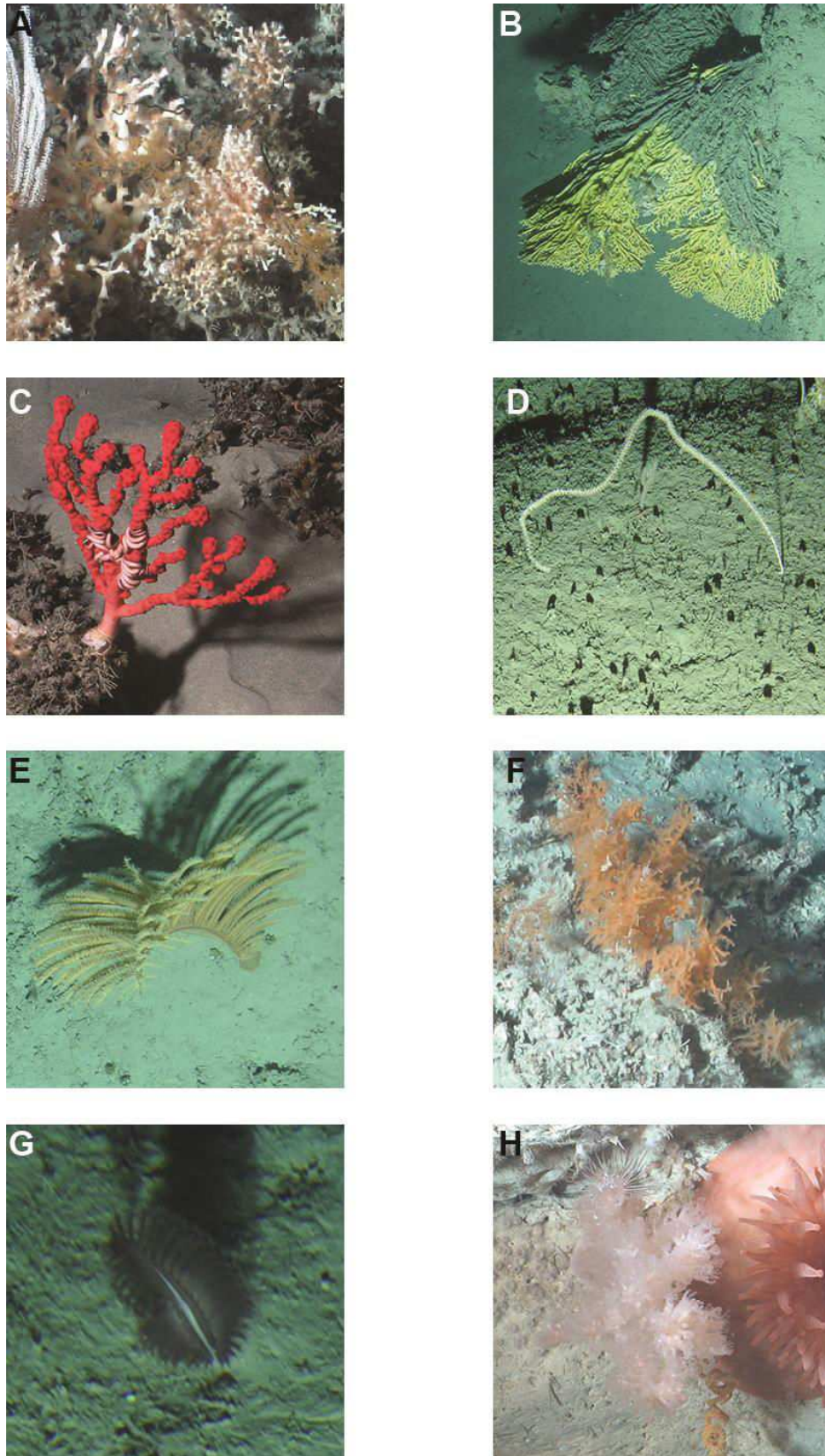


Figure 4: Examples of cold-water corals: (A) the colonial scleractinians *Lophelia pertusa* (left) and *Madrepora oculata* (right) (BobEco, 2011), (B) the colonial scleractinian *Enallopsammia rostrata* (Evhoe 2011), (C) the gorgonian *Paragorgia* sp. with an ophiuroid (BobEco, 2011), (D) the bamboo or Isididae gorgonian *Lepidisis* sp. (Evhoe 2011), (E) the antipatharian *Bathypathes* sp. (Evhoe 2011), (F) the antipatharian *Leiopathes* sp. (BobEco, 2011), (G) the sea pen *Pennatula* sp. (Evhoe 2011), and (H) a soft coral from the Alcyoniina Suborder (BobEco, 2011). Copyright of all images: Ifremer.

2.1. Scleractinians

2.1.1. Biology

Scleractinians have a calcareous (CaCO_3) exoskeleton and are therefore called stony corals. In total, almost 1500 scleractinian species are known in the world of which approximately 50% do not have a symbiosis with algae as tropical corals do and are, thus, azooxanthellate (Cairns, 2001; Cairns, 2007). Around 40% of all scleractinian species can be considered as deep-water scleractinian, occurring below 50 m water depth, of which approximately three-quarters are solitary, while the other form is colonial (Cairns, 2001; Cairns, 2007). Deep-sea scleractinians were already known to exist since the 18th century as they were brought up by fishermen (Cairns, 2001). It was also in this century that many scleractinian species were described, e.g. *Lophelia pertusa* and *Madrepora oculata* by Linnaeus (1758). *L. pertusa* and *M. oculata* are known for their reef-formations, particularly in the NE Atlantic, but other colonial scleractinians, e.g. *Solenosmilia variabilis*, *Goniocorella dumosa* and *Oculina varicosa*, can also be reef-building scleractinians (Freiwald *et al.*, 2004).

The majority of the scleractinians need hard substrate to settle (Cairns, 2007; Rogers, 1999). In multiple submarine canyons in the NE and NW Atlantic and the Mediterranean Sea, *L. pertusa*, *M. oculata*, *S. variabilis* and/or *Desmophyllum dianthus* were often observed on vertical walls and overhangs related to hydrodynamics (e.g. Fabri *et al.*, 2014; Gori *et al.*, 2013; Huvenne *et al.*, 2011; Morris *et al.*, 2013; Orejas *et al.*, 2009; Quattrini *et al.*, 2015; Robert *et al.*, 2015). Indeed, Gori *et al.* (2013) concluded that the preferred orientations of *L. pertusa* and *M. oculata* in Cap de Creus Canyon (Mediterranean Sea) were 90° and 135°, meaning that the colonies were growing on vertical features or under overhangs.

Scleractinians can be old; a specimen of *Enallopsammia rostrata* from the NE Atlantic was determined to be over 100 years old by radio carbon analysis (Adkins *et al.*, 2004). Growth rates were small, as usual in the deep sea. *L. pertusa* and *M. oculata* colonies grow 2 to 26 mm yr⁻¹, determined by aquarium experiments or investigations of scleractinians growing on oil and gas rigs (Bell and Smith, 1999; Gass and Roberts, 2006; Orejas *et al.*, 2008). Observed vertical extension rates of *E. rostrata* was 5 mm year⁻¹ (minimum) and *Desmophyllum cristagalli* between 0.5 and 2 mm year⁻¹ (Adkins *et al.*, 2004).

Scleractinians were primarily thought to be filter-feeders, catching mainly plankton and dissolved organic matter (Roberts *et al.*, 2009). Although the exact diet is not known, isotopic measurements of *L. pertusa*, *M. oculata* and *Leiopathes* spp. (antipatharian) specimens of the Logachev mound region (Rockall Bank, NE Atlantic) showed that the diet was similar to obligated filter-feeders, e.g. tunicates and bivalves, that fed upon relatively ‘fresh’ suspended particles (Duineveld *et al.*, 2007). However, *L. pertusa* could be an opportunistic feeder, using multiple sources of food, including dissolved organic matter (Mueller *et al.*, 2014), phytodetritus (Duineveld *et al.*, 2007), phytoplankton (Carlier *et al.*, 2009) and zooplankton (Carlier *et al.*, 2009; Duineveld *et al.*, 2004; Hebbeln *et al.*, 2014; Mienis *et al.*, 2012). Zooplankton is actively captured by the tentacles of the coral polyps. It reaches the corals by vertical migration (Hebbeln *et al.*, 2014; Mienis *et al.*, 2012). *L. pertusa* can even grow exclusively on zooplankton as shown in aquaria (Orejas *et al.*, 2008).

Most deep-water scleractinians are gonochoristic species, meaning that they have separated male and female colonies, e.g. the colonial scleractinians *O. varicosa* (Brooke and Young, 2003), *M. oculata*, *L. pertusa*, *G. dumosa*, *S. variabilis* and *E. rostrata* (Burgess and Babcock, 2005; Pires *et al.*, 2014; Waller and Tyler, 2005) and the solitary scleractinians *Fungiacyathus marenzelleri* (Flint *et al.*, 2007; Waller *et al.*, 2002), *Flabellum thouarsii*, *Flabellum curvatum* and *Flabellum impensum* (Waller *et al.*, 2008). The caryophyllids *Caryophyllia ambrosia*, *Caryophyllia cornuformis*, and *Caryophyllia sequenzae*, collected from Rockall Through and Porcupine Seabight, NE Atlantic, were cyclical hermaphroditic, meaning that one sex dominates at any one time (Waller *et al.*, 2005).

Scleractinians can reproduce asexually or sexually. The asexual reproduction can take place by budding, transverse division or fragmentation (Cairns, 1995; Highsmith, 1982; Roberts *et al.*, 2009). Budding means that a new genetically identical polyp is formed by growth and internal division of existing polyps or by developing new polyps from tissues adjacent to or between existing polyps (Harrison, 2011), expanding the existing colony or starting a new colony. Fragmentation is another form of asexual reproduction (Highsmith, 1982); a piece of the colony breaks off and settles on another place.

The sexual reproduction of deep-water scleractinians is largely unknown (Roberts *et al.*, 2009). However, broadcast spawning, releasing eggs and sperm into the water, is the most probable for most deep-water scleractinians: no planula (planktonic) larvae were seen in histological sections of reef-building scleractinians and the solitary scleractinian *F. marenzelleri* and species from the same families in shallow waters are also broadcast spawners (Brooke and Young, 2003; Burgess and Babcock, 2005; Roberts *et al.*, 2009; Waller *et al.*, 2002). The duration of larval period is unknown for deep-water scleractinians (Brooke and Järnegren, 2013), except for the colonial scleractinian *O. varicosa* and *L. pertusa* where larvae settle after 21 days and 3 to 5 weeks (up to 8 weeks), respectively (Brooke and Young, 2005; Larsson *et al.*, 2014). Brooding scleractinians do exist, i.e. the solitary scleractinians *F. thouarsii*, *F. curvatum* and *F. impensum* in Antarctic waters (Waller *et al.*, 2008), but this reproduction mode is relatively rare.

There is a large amount of evidence that the reproduction of marine organisms, including scleractinians, is controlled by external environmental factors (Brooke and Järnegren, 2013; Harrison, 2011). However, what these factors are and how they control the reproduction cycle of deep-sea invertebrates remains largely unknown (Brooke and Järnegren, 2013). Deep-sea scleractinians might respond to seasonal variations, especially the occurrences of planktonic blooms in the surface waters and, thus, food supply (Brooke and Järnegren, 2013). In Trondheim fjord, off Norway, *L. pertusa* may respond to the migration of the zooplanktonic species *Calanus finmarchicus* (Brooke and Järnegren, 2013). However, all year-round reproduction with a seasonal variation in intensity, so called quasi-continuous reproduction, does occur, as observed in *M. oculata* off Brazil, SW Atlantic (Pires *et al.*, 2014) and in Porcupine Seabight, NE Atlantic (Waller and Tyler, 2005), in *F. marenzelleri* off Scotland, NE Atlantic (Waller *et al.*, 2002), and in *C. ambrosia*, *C. cornuformis*, and *C. sequenzae* observed in Rockall Through and Porcupine Seabight, NE Atlantic (Waller *et al.*, 2005).

2.1.2. Distribution

Scleractinians occur in every Ocean, except for the Bering Sea and most of the Arctic Ocean (Cairns, 2007; Roberts *et al.*, 2006). Among the deep-water scleractinians the reef-forming species *L. pertusa* and *M. oculata* are the most known and studied in the North-East Atlantic, skewing the distribution of these two species and reef-building species in general (Fig. 5; Roberts *et al.*, 2006). However, other scleractinians, both solitary and colonial scleractinians, were also observed in the NE Atlantic and other Oceans and Seas in the world (Table 1). Some studies reported the habitat created by scleractinians (Table 1).

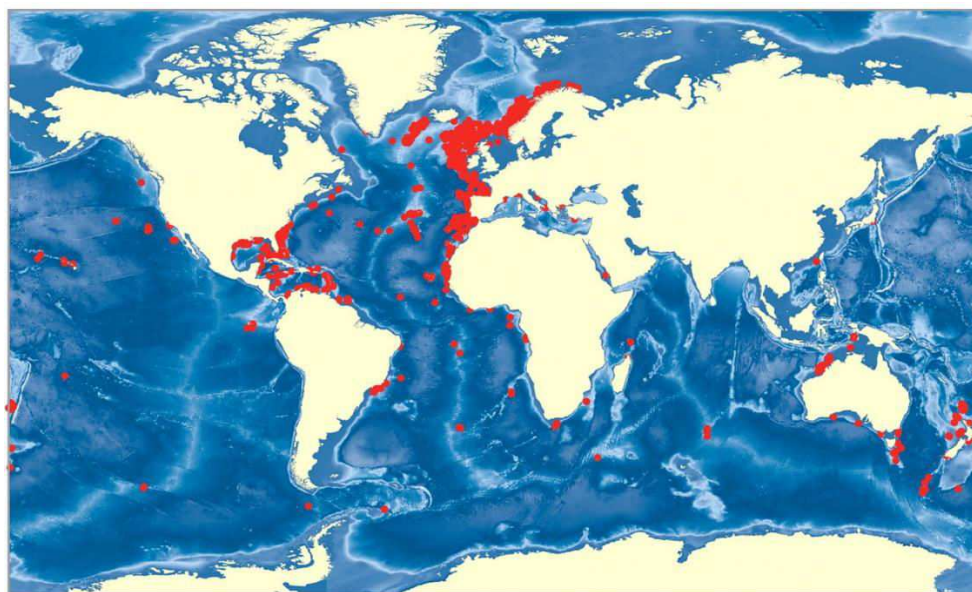


Figure 5: The distribution of reef-forming scleractinians. The red dots show records of reef-forming scleractinians using various sources. Sampling intensity is unknown. Reproduced from Roberts *et al.* (2006).

Scleractinians are observed on a range of geomorphic features, such as seamounts, submarine canyons, fjords and the continental shelf edge. The reefs off Norway are probably the most pristine cold-water coral reefs that are discovered until today (Flögel *et al.*, 2014; Mortensen *et al.*, 2001). They can be large and very high; the largest reef, Røst reef, with an approximate surface of 100 km², is also found off the coast of Norway (Freiwald, 2003; Mortensen *et al.*, 2001). On carbonate mounds, a structure with a biological origin, live colonies of *L. pertusa* and/or *M. oculata* are usually on the summit and can extend over large areas, as for example on Thérèse Mound in the Belgica Mound Province off Ireland (Huvenne *et al.*, 2005). Carbonate mounds are developed by the erosion and (re)colonisation of corals on the mounds (Roberts *et al.*, 2006). The Norwegian reefs and the reefs observed around the Faroe Islands, off Ireland and Scotland are dominated by *L. pertusa*. *M. oculata* is dominant over *L. pertusa* in the Mediterranean Sea, as observed in the Cap de Creus, Lacaze-Duthiers and Cassidaigne Canyons (Fabri *et al.*, 2014; Gori *et al.*, 2013; Orejas *et al.*, 2009) and the Santa Maria di Leuca Coral Province (Vertino *et al.*, 2010). In the Bay of Biscay, *M. oculata* and *L. pertusa* co-occur, with a slight dominance of *M. oculata* (Arnaud-Haond *et al.*, 2015; De Mol *et al.*, 2011) but on vertical walls in Whittard Canyon *L. pertusa* and/or *S. variabilis* were observed to be dominant (Huvenne *et al.*, 2011; Robert *et al.*, 2015).

Table 1: The occurrences of solitary and colonial scleractinians reported in the literature. This non-extensive list focused on the NE Atlantic and may concern species or the habitat formed by these scleractinian species, e.g. reef.

Region	Species	Habitat or species?	References
Off Norway	<i>L. pertusa</i> <i>M. oculata</i>	Habitat	Fosså <i>et al.</i> (2002); Mortensen <i>et al.</i> (2001)
Off Sweden	<i>L. pertusa</i> <i>M. oculata</i>	Habitat	Jonsson <i>et al.</i> (2004)
Along the Faroe Islands	<i>L. pertusa</i> <i>M. oculata</i> <i>S. variabilis</i>	?	Frederiksen <i>et al.</i> (1992)
Wyville-Thompson Ridge	<i>L. pertusa</i> <i>M. oculata</i>	Habitat	Howell <i>et al.</i> (2010)
Rockall Trough and Rockall Bank	<i>L. pertusa</i> <i>M. oculata</i> <i>S. variabilis</i> Solitary scleractinians	Habitat	Davies <i>et al.</i> (2015); Grehan <i>et al.</i> (2005); Robert <i>et al.</i> (2014)
Hatton Bank	<i>L. pertusa</i> <i>M. oculata</i> Solitary scleractinians	Habitat	Howell <i>et al.</i> (2010); Howell <i>et al.</i> (2011); Roberts <i>et al.</i> (2008)
Porcupine Seabight and Bank	<i>L. pertusa</i> <i>M. oculata</i>	Habitat	De Mol <i>et al.</i> (2007); Grehan <i>et al.</i> (2005); Henry and Roberts (2007); Huvenne <i>et al.</i> (2007); Huvenne <i>et al.</i> (2005)
Bay of Biscay	<i>L. pertusa</i> <i>M. oculata</i> <i>Dendrophyllia cornigera</i> Caryophyllids	Habitat Species	Altuna (2013); Davies <i>et al.</i> (2014); De Mol <i>et al.</i> (2011); Howell <i>et al.</i> (2010); Huvenne <i>et al.</i> (2011); Le Danois (1948); Morris <i>et al.</i> (2013); Reveillaud <i>et al.</i> (2008); Robert <i>et al.</i> (2015); Sánchez <i>et al.</i> (2014)
Galicia Bank	<i>L. pertusa</i> <i>M. oculata</i>	Habitat	Altuna (2013); Duineveld <i>et al.</i> (2004)
Gulf of Cadiz	<i>L. pertusa</i>	?	Wienberg <i>et al.</i> (2009)

	<i>M. oculata</i> <i>D. cornigera</i>		
Mid-Atlantic Ridge, including the Azores	<i>L. pertusa</i> <i>M. oculata</i> <i>S. variabilis</i> <i>Flabellum</i> sp.	Species	Braga-Henriques <i>et al.</i> (2013); Mortensen <i>et al.</i> (2008)
NW Atlantic	<i>L. pertusa</i> <i>M. oculata</i> <i>S. variabilis</i> <i>E. profunda</i> <i>D. dianthus</i>	Habitat	Brooke and Ross (2014); Cordes <i>et al.</i> (2008); Hebbeln <i>et al.</i> (2014); Kenchington <i>et al.</i> (2014); Quattrini <i>et al.</i> (2015); Tendal <i>et al.</i> (2013)
Mediterranean Sea	<i>L. pertusa</i> <i>M. oculata</i> <i>D. cornigera</i> <i>D. dianthus</i>	Habitat	Fabri <i>et al.</i> (2014); Gori <i>et al.</i> (2013); Orejas <i>et al.</i> (2009); Taviani <i>et al.</i> (2015); Vertino <i>et al.</i> (2010)
Off Brazil	<i>L. pertusa</i> <i>M. oculata</i> <i>S. variabilis</i> <i>E. rostrata</i> Solitary scleractinians	Species	Arantes <i>et al.</i> (2009); Sumida <i>et al.</i> (2004)

2.1.3. Environmental conditions

Scleractinian species are observed at all depths of the Ocean, but the majority, 85% of the azoonthellate scleractinians, are considered as deep-water species (Cairns, 2007). Scleractinians can reach depths until at least 4800 m in the NE Atlantic (Zibrowius, 1980). Reef-building species, especially *L. pertusa* and *M. oculata*, usually occur between 200 and 1000 m (Roberts *et al.*, 2006). Deep-water scleractinians and *L. pertusa* reefs can occur in waters with a temperature between 2 and 13°C (Freiwald *et al.*, 2004; Roberts *et al.*, 2006; Zibrowius, 1980), but *M. oculata* and the solitary scleractinians *Caryophyllia calveri* and *Stenocyathus vermiformis* can support temperatures of 15°C in the Mediterranean Sea (Zibrowius, 1980).

L. pertusa has been observed in waters with a salinity between 32 and 38 ‰/pss (Davies and Guinotte, 2011; Davies *et al.*, 2008; Freiwald *et al.*, 2004), whereas the salinity range in which *M. oculata*, *S. variabilis*, *G. dumosa* and *E. rostrata* were observed is smaller, from 34 to 37 pss (Davies and Guinotte, 2011). Dullo *et al.* (2008) observed a specific water density envelope of 27.35 to 27.65 kg m⁻³ for *L. pertusa* reefs in the NE Atlantic. This envelope may differ per region, as live *L. pertusa* occur in waters with a density of 27.1-27.2 kg m⁻³ in the Gulf of Mexico, NW Atlantic (Davies *et al.*, 2010), a density of 27.62-27.71 kg m⁻³ off the west coast of Greenland (Kenchington *et al.*, 2017) and a density of 28.80-29.35 kg m⁻³ in the Mediterranean Sea (Flögel *et al.*, 2014; Freiwald *et al.*, 2009; Gori *et al.*, 2013; Lo Iacono *et al.*, 2014; Taviani *et al.*, 2015).

Similarly, dissolved oxygen levels may also vary among regions, as the minimum dissolved oxygen level in which *L. pertusa* occurred, was much lower in the NW Atlantic (0.2 ml l⁻¹) than in the NE Atlantic (4.3 ml l⁻¹) (Davies *et al.*, 2008). There was a strong relationship between colonial scleractinian occurrences and the aragonite saturation horizon (Davies *et al.*, 2008; Roberts *et al.*, 2006), because scleractinians precipitate the calcium carbonate (CaCO₃) for their skeleton from the water (Cairns, 2007). The calcium carbonate concentration is, therefore, a limiting factor in deep-water coral occurrences and distribution (Cairns, 2007). *L. pertusa* was observed exclusively in aragonite saturated areas, what confirms this statement (Davies and Guinotte, 2011; Davies *et al.*, 2008).

The specific temperature and salinity values are linked with certain water masses in the water column. The density envelope of Dullo *et al.* (2008) corresponded to the Mediterranean Outflow Water (MOW). The *L. pertusa* reef off Greenland was associated with the Atlantic Water (AW) layer (Kenchington *et al.*, 2017). Seasonal variations in temperature and salinity of the water above the Greenland reef were observed, suggesting that vertical mixing at depth may occur in spring (Kenchington *et al.*, 2017). Vertical mixing is important for the transport of oxygen, nutrients and food from the surface to the deeper parts of the canyons (Huthnance, 1995; Kenchington *et al.*, 2017; Pingree and Mardell, 1985).

L. pertusa and *M. oculata* are observed in areas with turbulent hydrological regimes (e.g. Frederiksen *et al.*, 1992; Mortensen *et al.*, 2001; Roberts *et al.*, 2009; White *et al.*, 2005) that can cause this vertical mixing. The north-eastern flank of coral mounds in the Santa Maria di Leuca CWC Province (Mediterranean Sea) is exposed to the main current in this area (NE-SW direction) eroding this flank and transporting food particles. This flank was covered by

scleractinians, while the south-western flank was dominated by fine-grain sediment and coral colonies were rare or absent (Vertino *et al.*, 2010). Scleractinians benefit from the high currents in several ways; the current transports food with increasing quantities and quality to the corals and it prevents that the corals are getting buried or clogged by sediment (e.g. Roberts *et al.*, 2009). Several hydrological mechanisms can be responsible for the food supply. Internal waves and downwelling play a key role in the food supply (Davies *et al.*, 2009; Frederiksen *et al.*, 1992). Soetaert *et al.* (2016) showed that the morphology of the bottom changes the hydrological regime and therefore also the way food is supplied to corals. These authors have compared two areas of *L. pertusa*/*M. oculata*; one on the summit of a carbonate mound in the Logachev Mound region (600-1000 m water depth) and one on a ridge on the shelf break in the eastern part of Rockall Bank (400-500 m water depth). Two different hydrological mechanisms for organic matter supply were observed using a coupled model of hydro- and organic matter dynamics. It was suggested that these mechanisms were linked to the seafloor topography: on the mound, rapid downwelling was seen, especially during spring tide, bringing organic matter to the corals on the mound summits, while on the ridge, organic matter rich water was spilled over the continental shelf edge by similar processes as internal waves or dense shelf water cascading (Fig. 6) (Soetaert *et al.*, 2016). Downwelling, caused by tidal flows, was also an important process to transport organic matter to *L. pertusa* reefs at Mingulay Reef Complex and could have speeds up to 10 cm s^{-1} (Davies *et al.*, 2009). Advection of deep bottom water with a high suspended matter load onto the reef was another mechanism of food delivery to the CWC community (Davies *et al.*, 2009). The coral framework themselves could modify the bottom currents locally by the topography that they create, changing the velocity and direction, as it was observed on coral mounds in the Rockall Trough (Mienis *et al.*, 2007). In Whittard Canyon, food particles are laterally transported in the canyon by bottom currents from the shelf and interflues as well as by gravity flows and this transport may have an influence on the benthic communities in Whittard Canyon (Amaro *et al.*, 2015).

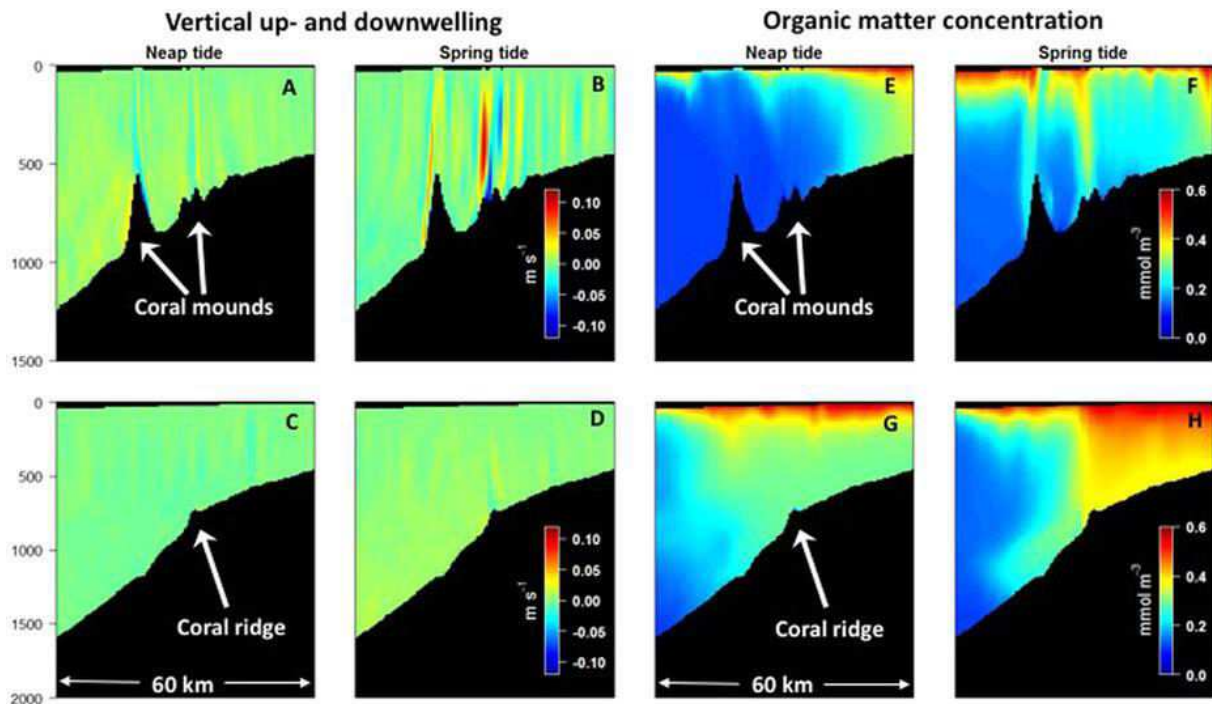


Figure 6: The model output of the current velocities (A-D) and the organic input (E-H) on coral mounds on Logachev Mounds Region (top) and a shelf-break ridge on Rockall Bank (bottom) during neap and spring tide. Reproduced from Soetaert *et al.* (2016).

Due to these hydrological processes, CWCs can be linked to primary production of surface waters. It was suggested that the absence of living scleractinians in the Gulf of Cadiz, NE Atlantic, was probably due to a low primary production and low tidal currents and thus reduced food supply at the seafloor (Wienberg *et al.*, 2009).

Filter-feeders, such as CWCs, rely on the quantity and quality of food transported by the current that may vary with current speeds. Capture rates of macro-plankton were measured in aquaria for *Dendrophyllia cornigera* and *L. pertusa* (Gori *et al.*, 2015; Purser *et al.*, 2010). The results showed increased capture rates by increasing current speed in *D. cornigera* (2, 5 and 10 cm s⁻¹; Gori *et al.*, 2015), while capture rates of *L. pertusa* were higher at current speeds of 2.5 cm s⁻¹ than at current speeds of 5 cm s⁻¹ (Purser *et al.*, 2010). It is possible that these differences are species related, but it may also suggest that CWCs may have an optimal speed to capture plankton.

Besides the influence of hydrology on the food supply, these processes also have an influence on larval dispersal, although this dispersal of scleractinians is poorly understood. The planktonic larvae of cold-water corals are thought to swim to the upper parts of the water column, including surface waters, as observed for *O. varicosa* and *L. pertusa* (Brooke and Young, 2003; Larsson *et al.*, 2014). The currents of the ocean, especially the surface currents, bring these larvae to other places, before the larvae become demersal. Genetic research of multiple *L. pertusa* reefs in Skagerrak, south of Norway, showed that the gene flow between the reefs was restricted, especially at a local scale in the northeastern part of Skagerrak (Dahl *et al.*, 2012). Over a larger area, the gene flow between reefs appeared also to be localised: (i) a moderate gene flow, with local recruitment of larvae, among *L. pertusa* populations from the Iberian margin to Scandinavian fjords was suggested by Le Goff-Vitry *et al.* (2004), where especially the fjord populations were highly genetically differentiated from the offshore regions

along the European margin, and (ii) the gene flow between populations in the Gulf of Mexico, off the southeastern coast of the US (NW Atlantic), two seamounts off New England (NW Atlantic) and three regions in the NE Atlantic (off UK and off Norway) was also restricted (Morrison *et al.*, 2011). Analysis of the genetic structure of these populations clustered them in three main clusters corresponding to the geographic location – Gulf of Mexico, off Southeastern US and the other locations in the North Atlantic Ocean (Morrison *et al.*, 2011). Within the North Atlantic Ocean cluster, two subpopulations were observed corresponding to the seamounts in the northwestern part and the locations in the NE Atlantic Ocean (Morrison *et al.*, 2011).

The complex local hydrology and geology are suggested as a reason for the gene flux/connectivity patterns at local and regional scales (Dahl *et al.*, 2012; Le Goff-Vitry *et al.*, 2004). However, larvae do have the ability to disperse over large geographic distances, as suggested by the connectivity results of *L. pertusa* populations in the Gulf of Mexico, the NW and NE Atlantic Ocean, where some genes were shared between these three regions (Morrison *et al.*, 2011) and ocean currents are playing a role in this dispersal. The pathways of dispersal could follow the main ocean currents linking the different parts of the Atlantic with each other. These ocean conveyor belts were also suggested to have an important role in the postglacial distribution expansion of *L. pertusa* by two dispersal events (Fig. 7; Henry *et al.*, 2014), what also explains the presence of the same species throughout the Atlantic. The recently observed live *L. pertusa* reef in the waters off Greenland is important for the biogeographic connection between the eastern and western Atlantic Ocean (Tendal *et al.*, 2013), potentially serving as stepping stone between these regions, although the genetic structure of this reef is not known. Currents are not only important for the larval dispersal, they also play a role in the larval settlement. Larsson *et al.* (2014) suggested that water movement was indeed one of the cues for *L. pertusa* larvae to settle on the bottom. If the velocity of the bottom currents is too high, it will erode the seafloor including the organisms (Levin *et al.*, 2001) and larvae do not have the opportunity to settle. Overall, the larval dispersal of scleractinians remains an area of research, especially because of its importance to conservation.

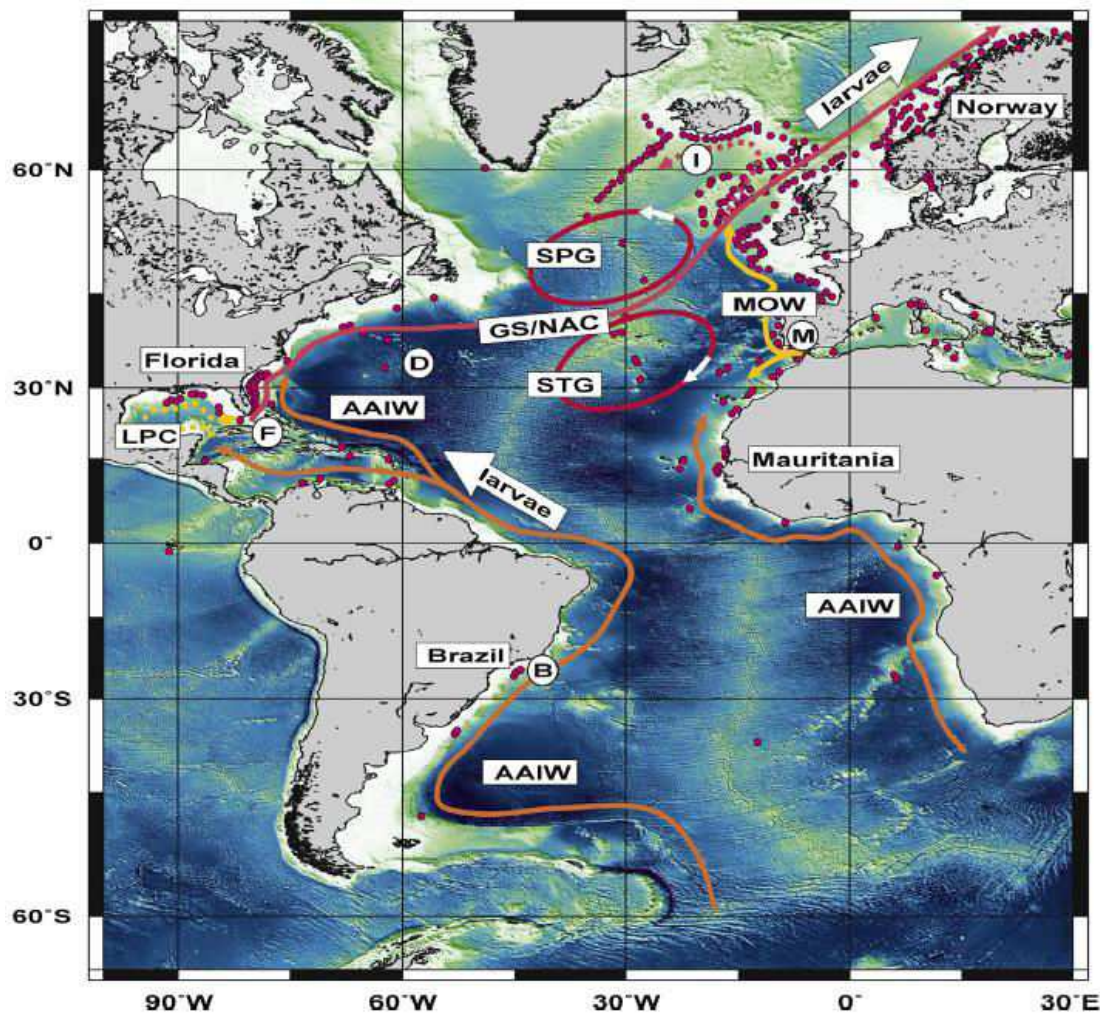


Figure 7: The present distribution of *Lophelia pertusa* in the Atlantic Ocean (red dots) in relation to simplified circulation features and proposed larval dispersal pathways. LPC = Loop Current; AAIW = Antarctic Intermediate Water; GS/NAC = Gulf Stream/North Atlantic Current; SPG and STG = subpolar and subtropical gyres; MOW = Mediterranean Outflow Water. The letters D and I indicate the deep and intermediate records of Atlantic meridional overturning circulation (AMOC) strength; the letters B, F and M indicate geochemical tracers of water mass history off Brazil, Florida and the Mediterranean, respectively. Reproduced from Henry *et al.* (2014).

2.1.4. Biodiversity of scleractinian reefs

Cold-water coral reefs are linked to a high biodiversity (Freiwald *et al.*, 2004; Roberts *et al.*, 2009), what is probably due to the heterogeneity formed by the three-dimensional framework (Buhl-Mortensen *et al.*, 2010; Mortensen *et al.*, 1995). Framework, whether it is alive or not, has a higher heterogeneity than coral rubble and bare substratum. Studies have distinguished four to six macrohabitats in coral reefs: (i) the living framework, (ii) the mostly dead framework that is clogged with sediment or loaded by detritus, (iii) coral rubble, (iv) (underlying) soft sediments (Mortensen *et al.*, 1995; Roberts *et al.*, 2006), (v) the cavities inside dead *L. pertusa* made by boring sponges and other bioeroders, and (vi) the free space between coral branches (Mortensen *et al.*, 1995).

The diversities between these macro-habitats differ, but is poorly quantified. Communities of macro- and megafauna associated with a high heterogeneity formed by live framework in

scleractinian reefs off Norway and the Gulf of Mexico or on the summit of carbonate mounds off Scotland and Sweden were more abundant and diverse than the communities of the macrohabitats on the low heterogeneous flanks of the coral mounds or intermediate areas of the reef, usually rubble, and the communities more distant from the reef/live summit (Cordes *et al.*, 2008; Henry and Roberts, 2007; Jonsson *et al.*, 2004; Mortensen and Fosså, 2006; Roberts *et al.*, 2008). The relation between abundance and/or diversity with the proportion of live coral cover was not always linear on a more local scale; in Norwegian offshore and inshore reefs, the abundance of macrofaunal species was highest in boxcore samples with a live coral cover of more than 20%, but the species diversity was higher in samples with a proportion of live *L. pertusa* between 1 and 20% (Mortensen and Fosså, 2006). The compositions of the both macro- and megafaunal communities on the reef/mound and off reef/mound also differ (Henry and Roberts, 2007; Jonsson *et al.*, 2004; Mortensen and Fosså, 2006). For example, deposit feeders were observed in higher densities in areas far from a Swedish reef than on the reef (Jonsson *et al.*, 2004). Similarly, more deposit feeders were observed in rubble areas off Norway (Mortensen and Fosså, 2006) or off coral mounds on Porcupine Seabight (Henry and Roberts, 2007) than on live reefs and on-mound areas. Suspension feeders, such as actinians, antipatharians and crinoids, dominated often the part of the reef with the most complex structure (Henry and Roberts, 2007; Jonsson *et al.*, 2004; Mortensen and Fosså, 2006).

The diversity of Norwegian and Scottish coral reefs could exceed the diversity of surrounding soft bottom areas as well as areas covered by coral rubble, i.e. broken pieces of scleractinians for macrofaunal (Buhl-Mortensen *et al.*, 2012; Henry and Roberts, 2007; Mortensen and Fosså, 2006), megafaunal (Buhl-Mortensen *et al.*, 2012; Mortensen *et al.*, 1995) and fish communities (Costello *et al.*, 2005; Husebø *et al.*, 2002). It is suggested that the community of CWC reefs may be more diverse than that of shallow-water reefs (e.g. Gheerardyn *et al.*, 2009; Henry *et al.*, 2008; Jensen and Frederiksen, 1992; Rogers, 1999) or at least the diversities may have a similar order of magnitude (Rogers, 1999). The high diversity of coral reefs is probably due to the functions the reefs may have for many organisms. This is especially important for fisheries and conservation, because the community on reefs also includes commercially important crustaceans and fish species (Freiwald *et al.*, 2004). Coral reefs provide **shelter**, as for example could be indicated by the high abundances of the squat lobster *Munida* within the scleractinian framework and rubble (Mortensen *et al.*, 1995) hiding for its predator, the tusk *Brosme brosme* (Husebø *et al.*, 2002). This interaction between prey and predator also indicates that coral reefs may serve as **feeding grounds**. Echinoids and gastropods were seen preying on the small organisms on the branches of *L. pertusa* and/or *M. oculata*, e.g. bacteria and foraminifera, the mucus secreted by these corals or the coral itself (Jensen and Frederiksen, 1992; Rogers, 1999; Stevenson and Rocha, 2013; Wild *et al.*, 2008). In addition, this habitat could also be important feeding grounds for non-predatory organisms: coral reefs are usually observed in high current areas and the framework provides filter- and suspension feeders an elevated position in the water column to benefit from these currents and the food particles in the potential nepheloid layer surrounding the coral reefs (Buhl-Mortensen *et al.*, 2010).

Coral reefs also serve as **reproduction and nursery areas**. Frederiksen *et al.* (1992) observed only juveniles to be associated to *L. pertusa* around the Faroe Islands. Norwegian *L. pertusa* reefs were rich of egg-cases of *Raja* sp. and pregnant females of *Sebastes* sp., a viviparous fish (Costello *et al.*, 2005; Fosså *et al.*, 2002; Husebø *et al.*, 2002). For this reason, coral reefs may

be important for fish. Indeed, some studies in the North-East Atlantic Ocean show that fish abundances were higher on coral reefs than outside the reef (Costello *et al.*, 2005; Husebø *et al.*, 2002; Linley *et al.*, 2016). Costello *et al.* (2005) calculated that 92% of the observed fish species and 80% of the observed individuals were associated to reefs and/or rubble fields near the reefs in the North-East Atlantic, that included Sula and Tautra reefs off Norway, Kosterfjord Sacken reefs off Sweden, the Darwin Mounds on Rockall Trough, SE Rockall Bank and NW Porcupine Bank and within Porcupine Seabight and the Hurtside shipwreck in the Faroe-Shetland Channel. However, Biber *et al.* (2014) observed no significant difference in the total fish abundance and biomass between on and off reefs or areas with coral framework. It is suggested that the relation between fish abundance and CWCs is species and/or region dependent (Auster, 2007; Biber *et al.*, 2014; Linley *et al.*, 2016). Off Norway, in the Rockall-Hatton Bank basin, Porcupine Seabight and the Bay of Biscay, tusks (*B. brosme*) and conger eels (*Conger conger*) were indeed more often observed on reefs than on non-reef areas (Biber *et al.*, 2014; Costello *et al.*, 2005; Linley *et al.*, 2016), whereas *Synaphobranchus kaupii* was associated with sediment dominated areas (Biber *et al.*, 2014; Costello *et al.*, 2005; Linley *et al.*, 2016). *Helicolenus dactylopterus* was primarily observed on coral areas on Rockall Bank compared to Hatton Bank and the Belgica Mounds (Porcupine Seabight) (Biber *et al.*, 2014). These functions provided by coral reefs as well as the presence of hard substratum, cause them to be **hotspots of biodiversity** (Buhl-Mortensen *et al.*, 2010; Jensen and Frederiksen, 1992; Roberts *et al.*, 2009) and **biomass** (Van Oevelen *et al.*, 2009). Ten years ago, 1300 species were recorded in *L. pertusa* reefs in the North-East Atlantic (Roberts *et al.*, 2006), but this number may have increased in the last decade due to new studies on areas that were not explored yet as well as the discovery of new species.

2.2. Antipatharians, gorgonians and sea pens

2.2.1. Biology

Even though antipatharians, gorgonians and sea pens cannot form reefs such as *L. pertusa* and *M. oculata* do, they are able to form aggregations that are often referred to as coral gardens or forests (Freiwald *et al.*, 2004). Antipatharians or black corals, belonging to the hexacorals, have a black proteinaceous skeleton (Cairns, 2007; Wagner *et al.*, 2012a). Gorgonians, belonging to the octocorals, have a calcareous axis (Watling *et al.*, 2011).

The classification of all antipatharians includes seven families, 40 genera and 235 species (Cairns, 2007; Daly *et al.*, 2007), of which 75% are observed deeper than 50 m and are considered as deep-water species (Cairns, 2007). The Pennatulacea includes 14 families and 200 valid species (Williams, 1995; Williams, 2011). Gorgonians (with supporting axis) and the soft corals (without supporting axis) belong to the same order Alcyonacea (Daly *et al.*, 2007; Watling *et al.*, 2011). This order includes 30 families and more than 2700 species in total distributed over two groups of gorgonians, the Calcaxonina and Holaxonina, and four “subordinal groups”, the Alcyoniina, Protoalcyonaria, Scleraxonina and Stolonifera (Daly *et al.*, 2007). The gorgonians include 10 families, 161 genera and approximately 1300 species (Daly *et al.*, 2007). Approximately 75% of all octocorals, including both Alcyonacea and Pennatulacea, are

considered as deep-water corals, occurring deeper than 50 m (Cairns, 2007), however, separated proportions for each of the octocorallian orders or suborders were not found in literature. The major families of the Alcyonacea living in the deep sea are Chrysogorgiidae, Isididae (or bamboo corals) and Primnoidae (Watling *et al.*, 2011).

Most antipatharians and gorgonians need hard substrate to settle, whereas most sea pens anchor in soft sediment (e.g. Roberts *et al.*, 2009; Wagner *et al.*, 2012a; Williams, 2011). Exceptions are a few species of the antipatharian genera *Bathypathes* and *Schizopathes* (Wagner *et al.*, 2012a) as well as the gorgonian family Isididae, which can occur also on soft sediment (Mortensen and Buhl-Mortensen, 2005; Williams, 1995). A few pennatulid species, such as *Anthoptilum* sp., are able to settle on rocky substrate (Williams, 2011).

Age determinations by radiocarbon dating of a *Leiopathes glaberrima* colony (antipatharian) indicated an age of approximately 2000 years (Bo *et al.*, 2015). However, another specimen of *Leiopathes* sp. with an estimated age of over 4000 years is probably the oldest living record until so far (Roark *et al.*, 2009). Gorgonians can also be very old; a specimen of *Keratoisis ornata* collected off Canada had an age of approximately 200 years (Sherwood and Edinger, 2009).

Growth rates of CWCs are rarely determined, but usually gorgonians, antipatharians and sea pens grow slow. Various species of isidid gorgonians or bamboo corals were estimated to have radial growth rates, increasing the radius of the coral ‘stem’, of less than 0.1 mm yr⁻¹ (Sherwood and Edinger, 2009; Thresher, 2009). Estimations of radial growth for other gorgonians, *Lepidisis* spp., *Primnoa resedaeformis*, *Primnoa pacifica*, *Paragorgia arborea* and *Paramuricea* spp., were variable ranging between 0.04 to 0.32 mm year⁻¹ (Roberts *et al.*, 2009 and references herein; Sherwood and Edinger, 2009). Axial growth rates or vertical growth, increasing the axis of the coral, were usually larger than radial growth. Estimated axial growth rates of specimens of *P. resedaeformis*, *P. pacifica*, *Paramuricea* spp., and *P. arborea* ranged between 0.2 and 2.6 cm yr⁻¹ (Roberts *et al.*, 2009 and references herein; Sherwood and Edinger, 2009).

For deep-water antipatharians, the radial growth rates were also much smaller than the vertical growth (Wagner *et al.*, 2012a). Radial growth rates of deep-water antipatharians were also very variable, ranging from only 0.005 mm year⁻¹ (*Leiopathes* spp.) to 0.1 mm year⁻¹ (*Antipathella fiordensis*) and included the species *Leiopathes* spp., *A. fiordensis* and *Stauropathes arctica* (Roberts *et al.*, 2009; Sherwood and Edinger, 2009; Wagner *et al.*, 2012a). Vertical growth rates of *S. arctica* and *A. fiordensis* were estimated on approximately 1.2-1.4 and 1.3-1.8 cm yr⁻¹, respectively (Sherwood and Edinger, 2009; Wagner *et al.*, 2012a).

Colonies of gorgonians, antipatharians and pennatulaceans can become very tall. Sizes of pennatulaceans are highly variable, but some species, e.g. *Funiculina quadrangularis*, *Umbellula* sp. and *Halipteris willemoesi* can form colonies between 1 and 3 meters (Williams *et al.*, 2014). Antipatharians can be at least 2 m (Bo *et al.*, 2015); in New Zealand, 4 to 5 m tall colonies of the antipatharian *Bathypathes platycaulus* were reported (Smith, 2001). A colony of the gorgonian *Paragorgia* spp. up to 10 m in height was also reported for New Zealand (Smith, 2001).

Growth rate data for pennatulaceans are rare. However, similarly to gorgonians and antipatharians, they are suggested to grow only a couple of millimetres per year. The average growth rates of samples from the pennatulacean *Halipteris finmarchica* collected off Canada in

the NW Atlantic was $0.13 \text{ mm year}^{-1}$ in diameter and 4.9 cm year^{-1} in linear direction (De Moura Neves *et al.*, 2015b).

Gorgonians feed on live particulate organic matter (Orejas *et al.*, 2003) and their diet can include phyto- and zooplankton (Carlier *et al.*, 2009). At a *L. pertusa*/*M. oculata* reef in the Santa Maria di Leuca Coral Province (Mediterranean Sea), the diet of the antipatharian *L. glaberrima* included phytoplankton and contained less zooplankton than scleractinians (*L. pertusa*, *M. oculata* and *D. dianthus*) and a gorgonian species (*Paramuricea* cf. *macrospina*) as shown by stable isotope analysis (Fig. 8) (Carlier *et al.*, 2009). However, the diet of octocorals and antipatharians remains largely unknown, but it may differ among species. Differences in diet was suggested to cause a high abundance of the gorgonian *Leptogorgia sarmentosa* in a more sheltered area of Cape of Creus region (Mediterranean Sea) compared to hotspots of the other gorgonian species *Eunicella singularis* and *Paramuricea clavata* that occurred in a more current-exposed area (Gori *et al.*, 2011). This could suggest that these gorgonians have a different trophic niche and that this niche might explain their spatial separation.

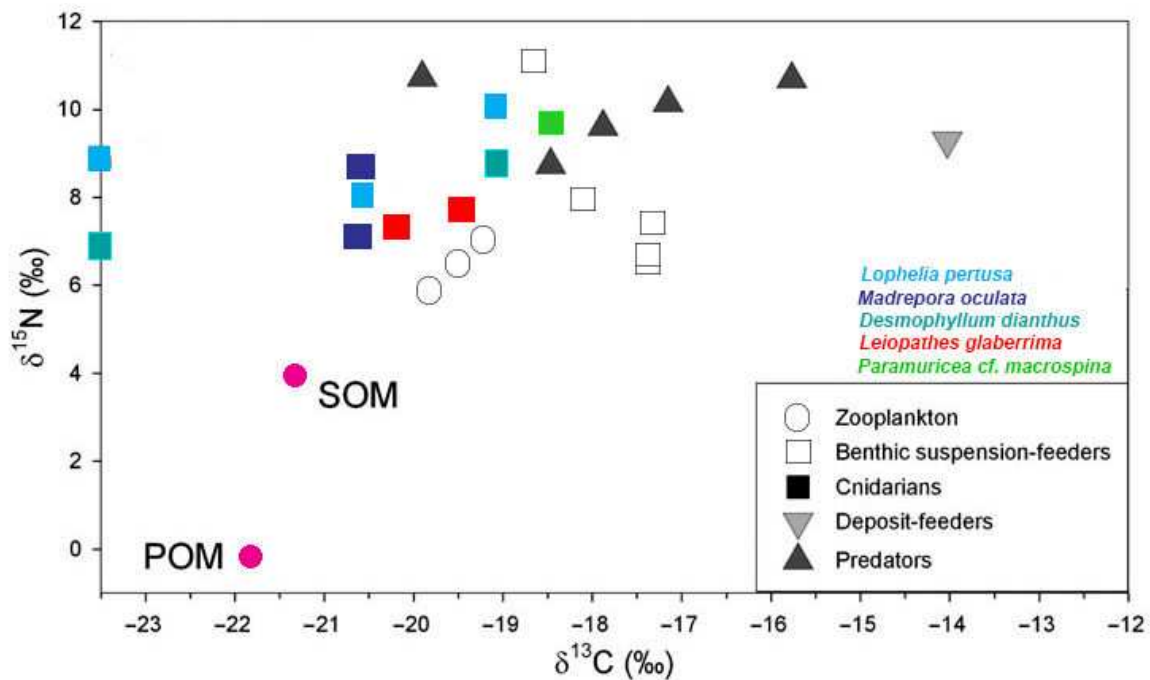


Figure 8: A diagram showing the stable isotope composition ($\delta^{13}\text{C}$ versus $\delta^{15}\text{N}$) of suspended organic matter (pink; SOM), particulate organic matter (pink; POM) and the samples of consumers collected at Santa di Leuca CWC Province (Mediterranean Sea). The different coral species (solid square) are indicated by colours: the scleractinian *Lophelia pertusa* in light blue, the scleractinian *Madrepora oculata* in dark blue, the scleractinian *Desmophyllum dianthus* in dark-cyan, the antipatharian *Leiopathes glaberrima* in red and the gorgonian *Paramuricea* cf. *macrospina* in green. Modified from Carlier *et al.* (2009).

Studies reporting on the reproduction of these types of corals are scarce. However, it is known that the reproduction can be asexual or sexual, similar to scleractinians (Wagner *et al.*, 2012a; Wagner *et al.*, 2011). Budding is the most important asexual reproduction for antipatharians, but they could form new colonies by fragmentation (Wagner *et al.*, 2012a). Since a limited number of studies to deep-water antipatharians has been undertaken, data on shallow-water antipatharians are included in this section. Asexual reproduction in deep-sea octocorals has

never been observed yet (Watling *et al.*, 2011), so, if they do reproduce asexually, this type of reproduction is very rare.

Similar to scleractinians, the majority of octocorals are gonochoric (reviewed by Kahng *et al.*, 2011 and Watling *et al.*, 2011). The separation of male and female colonies has been observed in several shallow- and deep-water antipatharians, deep-water gorgonians and deep-water pennatulaceans (**shallow-water antipatharians** *Antipathes grandis*, *Antipathes griggi*, *Cirrhipathes* cf. *anguina*, *Stichopathes echinulata*, *Aphanipathes verticillata*: Wagner *et al.*, 2012b; Wagner *et al.*, 2011; and *Antipathes fiordensis*: Parker *et al.*, 1997; **deep-water antipatharian** *Bathypathes alternata*: Wagner *et al.*, 2012b; Wagner *et al.*, 2011; **deep-water gorgonians**: *Acanella arbuscula*: Beazley and Kenchington, 2012; *P. clavata*, *E. singularis*: Gori *et al.*, 2007; *Primnoa notialis*, *P. pacifica*, *Swiftia beringi*, *Swiftia kofoidi*, *Swiftia pacifica*, *Swiftia simplex*, *Swiftia spauldingi* and *Swiftia torreyi*: Feehan and Waller, 2015; *P. resedaeformis* and *K. ornata*: Mercier and Hamel, 2011; *Dasystenella acanthina*, *Fannyella rossii*, *Fannyella spinosa* and *Thouarella* sp.: Orejas *et al.*, 2007; **deep-water pennatulaceans**: *H. finmarchica*: Baillon *et al.*, 2015; *Anthoptilum grandiflorum*: Baillon *et al.*, 2014; *Anthoptilum murrayi*: Pires *et al.*, 2009; *F. quadrangularis*: Edwards and Moore, 2009; *Pennatula phosphorea*: Edwards and Moore, 2008).

Further, it is thought that most deep-water antipatharians, gorgonians and pennatulaceans are broadcast spawners, similar to most scleractinians. The few existing studies showed an absence of planula larvae in these corals, e.g. the gorgonians *A. arbuscula*, *D. acanthina*, two Pacific gorgonians from the *Primnoa* genus and six Pacific gorgonians from the *Swiftia* genus (Beazley and Kenchington, 2012; Feehan and Waller, 2015; Orejas *et al.*, 2007), the pennatulaceans *F. quadrangularis*, *H. finmarchica*, *A. grandiflorum*, *A. murrayi* and *P. phosphorea* (Baillon *et al.*, 2015; Baillon *et al.*, 2014; Edwards and Moore, 2008; 2009; Pires *et al.*, 2009) and the antipatharians *A. fiordensis* (Parker *et al.*, 1997), *A. grandis*, *A. griggi*, *C. cf. anguina*, *S. echinulata*, *A. verticillata* and *B. alternata* (Wagner *et al.*, 2012a; Wagner *et al.*, 2012b; Wagner *et al.*, 2011). The gorgonians *P. resedaeformis* and *K. ornata* are also broadcast spawners, as suggested by Mercier and Hamel (2011), even though the authors are not clear about an absence of planula larvae. In addition, most shallow water octocorallian species are also broadcast spawners (Kahng *et al.*, 2011; Watling *et al.*, 2011). Sea pens may be exclusively broadcast spawners, whereas soft corals (Alcyonacea) also includes brooding species, consistently in the two families of true soft corals (Alcyoniina) and gorgonians in the arctic (Watling *et al.*, 2011). Brooding octocorallian species can adopt two forms of brooding: internal and external (Kahng *et al.*, 2011). Orejas *et al.* (2007) observed larvae in the gastrovascular cavities of three arctic gorgonians *Thouarella* sp., *F. rossii* and *F. spinosa*, indicating that these gorgonians may release larvae and thus have an internal brooding strategy. External brooding means that the fertilization and brooding takes place on the external surface of the female colony (Watling *et al.*, 2011).

The reproduction of octocorals could be triggered by environmental factors, of which an increase in water temperature and the coinciding planktonic bloom are probably the most important. The increase of water temperature is most likely the trigger to spawn in *P. phosphorea*, and the control of planktonic blooms coinciding in the same period is discussed for this species (Edwards and Moore, 2008). The spawning of *F. quadrangularis* is also influenced by seasonal indicators, but these may be different factors as other sea pens, since

this species is observed to release the gametes in late autumn/winter instead of in summer (Edwards and Moore, 2009). The suspended particulate material (SPM) in the water, rather than the primary production, appeared more important for the spawning of the arctic, but shallow-water sea pen, *Malacobelemnion daytoni* (Servetto and Sahade, 2016). Populations of the same species at different locations separated by several 100s of km, could spawn at different times, due to local variations in the environmental trigger. A shift in the spawning period of populations of the pennatulaceans *H. finmarchica* and *A. grandiflorum* off Newfoundland and Labrador (Canada) from the south to the north is observed following the period of planktonic blooms and temperature changes of the water (Baillon *et al.*, 2015; Baillon *et al.*, 2014). Similarly, a shift in spawning was also observed for populations of the gorgonians *P. clavata* and *E. singularis* at two locations in the Western Mediterranean Sea, relating to a difference in timing of a temperature increase and a planktonic bloom at the two regions (Gori *et al.*, 2007). A year-round reproduction is more likely for the gorgonian *A. arbuscula*, although a peak in numbers of large oocytes have been observed in October (Beazley and Kenchington, 2012). Similarly, it was suggested that the sea pen *A. murrayi* also has a continuous reproduction (observed off Brazil), instead of seasonal variations, unlike many other sea pens (Pires *et al.*, 2009).

Seasonality in antipatharian reproduction has been studied only in shallow water antipatharians and were linked to temperature variations (see Wagner *et al.*, 2012a and references herein). The reproduction of *A. griggi* off the Hawaiian Islands responded to temperature fluctuations of the water (Wagner *et al.*, 2012b) and the reproduction of *A. fiordensis* in a New Zealand fjord was also highly seasonal (Parker *et al.*, 1997).

2.2.2. Distribution

Non-scleractinian CWC species are also observed in all oceans. Antipatharians and octocorals (including gorgonians and sea pens) are widespread and found in all oceans from tropical to polar waters (Fig. 9; Table 2) (Wagner *et al.*, 2012a; Watling *et al.*, 2011; Williams, 1995).

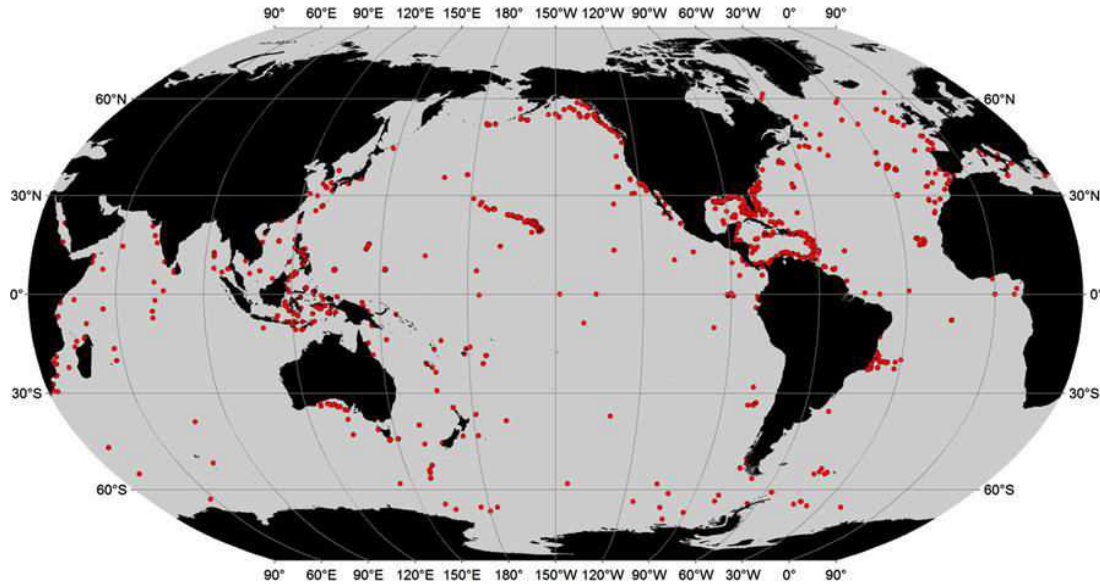


Figure 9: Distribution of antipatharians using records from the literature and museum specimen housed in the National Museum of Natural History, Smithsonian Institution. Sampling intensity is unknown. Reproduced from Wagner *et al.* (2012a).

Table 2: the distribution of antipatharians, gorgonians and sea pens. This non-extensive list focuses on the north Atlantic and may concern species or the habitat formed by these CWCs, e.g. coral garden.

Region	Antipatharians	Gorgonians	Sea pens	Habitat or species?	References
Norway		√		Species	Buhl-Mortensen <i>et al.</i> (2015); Buhl-Mortensen and Buhl-Mortensen (2014)
Iceland		√		Species	Buhl-Mortensen <i>et al.</i> (2015)
Faroe Islands		√		Species	Buhl-Mortensen <i>et al.</i> (2015)
Rockall Trough and Rockall Bank	√	√		Habitat	Davies <i>et al.</i> (2015)
Bay of Biscay	√	√	√	Habitat Species	Davies <i>et al.</i> (2014); Howell <i>et al.</i> (2010); Le Danois (1948); Morris <i>et al.</i> (2013); Robert <i>et al.</i> (2015)
Gulf of Cadiz	√	√		Habitat	Wienberg <i>et al.</i> (2009)
Mid-Atlantic Ridge, incl. the Azores	√	√	√	Species	Braga-Henriques <i>et al.</i> (2013); Mortensen <i>et al.</i> (2008)
NW Atlantic	√	√	√	Habitat Species	Baker <i>et al.</i> (2012); Kenchington <i>et al.</i> (2014); Mortensen and Buhl-Mortensen (2005); Murillo <i>et al.</i> (2011); Quattrini <i>et al.</i> (2015)
Mediterranean Sea	√	√	√	Habitat Species	Bo <i>et al.</i> (2015); Fabri <i>et al.</i> (2014); Gori <i>et al.</i> (2011); Mastrototaro <i>et al.</i> (2013)
Arctic		√		Habitat	Buhl-Mortensen <i>et al.</i> (2015); De Moura Neves <i>et al.</i> (2015a)

2.2.3. Environmental conditions

The environmental conditions of antipatharians, gorgonians and pennatulaceans are largely unknown, since most of the studies investigated reef-building scleractinians. These non-scleractinian corals are observed on large depth ranges. Pennatulaceans are present from the shelf down to more than 6000 m water depth (Williams, 1995; Williams, 2011). Antipatharians are observed until as deep as 8600 m in the North-western Pacific (see Wagner *et al.*, 2012a). Gorgonians are known to occur in water depths more than 8000 m, but most of the species have been recorded above 2000 m water depth (Yesson *et al.*, 2012). The seawater below 50 m water depth where deep-water octocorals occur had a mean water temperature of 5 and 11°C depending on the coral suborder, e.g. *Calcaxonia* (gorgonian suborder) and *Sessiliflorae* (sea pen suborder) (Yesson *et al.*, 2012). Octocorals occurred in salinities of approximately 34 to 36 pss and in waters with a dissolved oxygen concentration between approximately 3 and 7 ml l⁻¹ (Yesson *et al.*, 2012).

The water temperature of deep-water antipatharians (records below 50 m water depth) was usually between 0 and 10°C, but could be up to 25°C (Yesson *et al.*, 2015). Antipatharians occur in water with salinities of approximately 34 to 36 pss and a dissolved oxygen concentration between 1 to 7 ml l⁻¹ (Yesson *et al.*, 2015).

Hydrodynamics are also important for antipatharians, gorgonians and pennatulaceans, as it is for scleractinians. Also for these coral types, the currents transport food particles to the coral polyps. Further, the larval dispersal is influenced by the hydrodynamics, even though the larval dispersal of octocorals and antipatharians is largely unknown. Dispersal models based on genetics showed a low connectivity between populations of the antipatharian *L. glaberrima* at Viosca Knolls and at Green Canyon, located respectively west and east of Mississippi Canyon, in the Gulf of Mexico (Cardona *et al.*, 2016). Similar dispersal models, but based on physical traits, revealed that the dispersal from east to west (and vice versa) is limited by the bathymetric complexity of the seafloor between these locations and the differences in current direction to the east and west of the canyon, and by flow instabilities, generated by the complex bathymetry of the continental shelf and slope of the Gulf of Mexico (Cardona *et al.*, 2016). It may be possible that Mississippi Canyon, located between the two regions, forms a physical barrier for larval dispersal of *L. glaberrima*. In addition to hydrodynamics and geomorphology, other processes that occur before or after the settlement of a larvae on the seafloor, e.g. duration of larval stage and mortality, are important for larvae dispersal (Cardona *et al.*, 2016). The duration of the planulae larval stage of the gorgonian *P. clavata* was 3 to 15 days in the laboratory (Linares *et al.*, 2008). The post-settlement mortality of this species was very high in field experiments; none of the settled polyps survived for more than 7 months in both years of observation (Linares *et al.*, 2008). In general, octocorals appear to have a smaller dispersal compared to scleractinians as could be seen from their distribution patterns (Kahng *et al.*, 2011). Larvae of the shallow-water New Zealand *A. fiordensis* are weak swimmers, are negatively buoyant and have a short duration of the larval stage (Parker *et al.*, 1997). The hydrodynamics that can be restricted from place to place further limits the larval dispersal of this species, which is the case in the fjords southwest of New Zealand, increasing genetic differences between

populations (Miller, 1997). It is unlikely that *A. fiordensis* larvae can move over distances longer than 10 km (Miller, 1997, 1998).

2.2.4. Biodiversity

Even though the number of studies of non-scleractinians CWCs and the habitats they form are low, coral gardens and sea pen fields may have similar functions as scleractinian reefs. In fact, these species do create a heterogeneity in areas where the seafloor relief otherwise is low, especially in sandy or muddy areas (Buhl-Mortensen *et al.*, 2010; Tissot *et al.*, 2006). Habitat heterogeneity could increase both density and diversity but also change the species composition of the coral community (Hargrave *et al.*, 2004; Henry and Roberts, 2007; Robert *et al.*, 2014). Gorgonians, antipatharians and sea pens might give organisms protection to predators (**shelter**) (Buhl-Mortensen and Mortensen, 2005; Buhl-Mortensen *et al.*, 2010). *Munida* sp. observed off Norway used sea pens as protection for predators, probably because of the stinging cells and the bioluminescence of the sea pens that would scare the predators (De Clippele *et al.*, 2015). Another squat lobster, *Gastroptrychus formosus*, preferred to associate with the antipatharian *Leiopathes* sp., but was also seen on the antipatharian *Bathypathes* sp. and the gorgonian *Paramuricea* sp. on five sites off Ireland (Le Guilloux *et al.*, 2010). This association may protect the squat lobster, but it may also be possible that the squat lobster feed on particulate organic matter and zooplankton trapped in mucus secreted by the antipatharians and gorgonians (Le Guilloux *et al.*, 2010). The use of coral gardens as **feeding grounds** could also be indicated by the higher position of euryalid ophiuroids and crinoids on antipatharians and octocorals. These filter-feeders, thus, has a better position in the current and/or nepheloid layer to capture food or have access to the food captured by the coral itself (Buhl-Mortensen *et al.*, 2010; De Clippele *et al.*, 2015; Grange, 1991). Examples of associations between filter-feeders and corals can be given by the association between the ophiuroid *Astrobrachion constrictum* and the antipatharian *A. fiordensis* in New Zealand (Grange, 1991) and the association between the ophiuroid *Gorgonocephalus* spp. and the gorgonians *P. arborea*, *P. resedaeformis* and *Paramuricea placomus* as well as the ophiuroid *Asteryx loveni* with the sea pen *F. quadrangularis* (De Clippele *et al.*, 2015). Amphipods on gorgonians, also off Norway, were observed to be feeding, indicated by moving mouth parts, but it was not known on what they were feeding (De Clippele *et al.*, 2015). The zooplanktivorous spider crab *Rochinia rissoana* (accepted as *Anamathia rissoana*; see World Register of Marine Species WoRMS, www.marinespecies.org) was observed in the living and erected part of the CWC colonies in Santa Maria di Leuca CWC Province (Carlier *et al.*, 2009) and may thus benefit from the higher position in the water column.

Sea pens may function as nursery areas for fish species as indicated by the fish larvae, e.g. *Sebastes* spp, associated to them (Baillon *et al.*, 2012). Egg cases of catsharks were also observed to be attached to the gorgonian *Calligorgia* sp. in the Mississippi Canyon, Gulf of Mexico, NW Atlantic (Etnoyer and Warrenchuk, 2007).

Sea pens are also known to share their habitat with burrowing megafauna. The commercially important langoustine *Nephrops norvegicus* was observed to be in areas of *F. quadrangularis* in Mediterranean submarine canyons (Fabri *et al.*, 2014). However, the reason behind this association is not known.

Very few studies compared the diversity associated to gorgonian and antipatharian coral gardens and sea pen fields to coral reefs. However, sea pen and *A. arbuscula* gorgonian communities were estimated to be less diverse than a habitat constructed by dense *L. pertusa* colonies on a vertical wall in Whittard Canyon (Robert *et al.*, 2015) and *L. pertusa* reef on Anthon Dohn Seamount, Rockall Trough (Davies *et al.*, 2014).

3. Anthropogenic impact

Human activities are increasing in the deepest parts of the ocean, due to depletion in resources on land and in shallower waters (Ramirez-Llodra *et al.*, 2011). However, each type of human activity, whether it is drilling for oil and gas, fishing or tourism, leaves a footprint on marine ecosystems. Impacts of litter, the fishing industry and climate changes are the biggest threats to CWCs.

3.1. Litter

Marine litter is defined as “any persistent, manufactured or processed solid material discarded, disposed of or abandoned in the marine and coastal environment” (UNEP, 2009). A description of marine litter on the seafloor is important for management strategies; e.g. litter is one of the descriptors of Good Environmental Status (GES) within the European Marine Strategy Framework Directive (Galgani *et al.*, 2013). Many items can be considered as litter, of which plastics are the most common (e.g. Galgani *et al.*, 2015; Pham *et al.*, 2014b; Ramirez-Llodra *et al.*, 2013). Litter in the deep sea is increasingly reported in literature being widely distributed in every ocean. The seafloor is a large sink for litter (Galgani, 2015; Galgani *et al.*, 1995), even though litter has a heterogeneous distribution over the seafloor (Pham *et al.*, 2014b; Ramirez-Llodra *et al.*, 2013).

Hydrodynamics control the circulation, distribution and accumulation of litter (Galgani *et al.*, 2000; Mordecai *et al.*, 2011; Pham *et al.*, 2014b). Plastics can reach the most remote and deepest parts of the oceans that are located far from their entry point due to currents. Miyake *et al.* (2011) observed litter as deep as 7216 m in the Ryukyu Trench near Japan and Bergmann and Klages (2012) observed litter items on video surveys near Svalbard in the Arctic.

Submarine canyons act as a conduit for litter, transporting items from the continental shelf to the deep sea (Galgani *et al.*, 2015; Galgani *et al.*, 2000; Galgani *et al.*, 1996; Mordecai *et al.*, 2011; Pham *et al.*, 2014b; Ramirez-Llodra *et al.*, 2011; Schlining *et al.*, 2013) as it does for sediments. Pham *et al.* (2014b) found that litter abundance was higher in submarine canyons than on other geomorphic settings, such as continental shelves and seamounts. The presence of tidal currents along the slope of canyons as well as other hydrological processes causes litter to accumulate within this geomorphic feature (Galgani *et al.*, 1996; Mordecai *et al.*, 2011; Pham *et al.*, 2014b; Ramirez-Llodra *et al.*, 2013; Schlining *et al.*, 2013). The hydrodynamics also played an important role in the distribution of litter on a coral mound in the Santa Maria di Leuca CWC Province off Italy in the Mediterranean Sea: plastic bags were mainly observed on

the flank that was exposed to the dominant current and tangled the coral colonies (K. Olu; pers. com), that covered this flank (Vertino *et al.*, 2010).

Local geomorphology is also important for the distribution of litter. Seafloor roughness can trap litter and prevent it from moving (Galgani *et al.*, 2015; Schlining *et al.*, 2013). The presence of complex geological and/or biological features increases the roughness of the seafloor by their three-dimensional structure. More litter was observed in areas with rocky outcrops, depressions and other geological features than on areas without these geological structures in two studies: off central and southern California (Watters *et al.*, 2010), and in Monterey Canyon (Schluning *et al.*, 2013). Biological features, such as corals and sponges, could also trap litter, as observed in areas covered by *Cladorhiza gelida* sponges (Bergmann and Klages, 2012).

Litter densities in canyons of the North-East Atlantic Ocean and the Mediterranean Sea, based on trawl or imagery data, are high and exceed more than thousands of items per km² (e.g. Mordecai *et al.*, 2011; Pham *et al.*, 2014b; Ramirez-Llodra *et al.*, 2013; Tubau *et al.*, 2015). Litter can have both a terrestrial and a maritime origin. Rivers transport litter, especially light plastics, to the ocean. This connection was clearly visible at the extensions of the Rhone and the Tordera Rivers in the western Mediterranean Sea (Galgani *et al.*, 2000; Ramirez-Llodra *et al.*, 2013; Tubau *et al.*, 2015) and at the Gironde estuary in the Bay of Biscay (Galgani *et al.*, 1995). A narrow continental shelf and coastal canyons could be linked with higher concentrations in these canyons compared to canyons incising a wider continental shelf. Indeed, higher concentrations were observed in the coastal canyons around Lisbon compared to other Portuguese canyons (Mordecai *et al.*, 2011) and in canyons in the Ligurian Sea that are close to the coast, compared to those in the Gulf of Lion (Fabri *et al.*, 2014). The precise origin of the items can be difficult to determine, except for items that are clearly used at sea, such as fishing gear or rapidly sinking products, e.g. glass bottles and clinkers (Ramirez-Llodra *et al.*, 2013). A relation between major shipping lanes and the abundance of litter on the deep seafloor was observed in the Mediterranean Sea (Ramirez-Llodra *et al.*, 2013).

Even though the impacts of litter by smothering, entanglement and ingestion to organisms are described (reviewed by Kühn *et al.*, 2015), the extent of this impact is not known yet. Entanglement of coral colonies with plastics and other marine litter causing the death or partial death of CWC colonies were reported in the literature (reviewed by Kühn *et al.*, 2015). The smothering and suffocation of cold-water corals are caused by litter, especially plastic bags and sheets, covering these organisms. Besides, litter can also induce sediment anoxia, with changes in the infaunal community because the exchange of pore water and the water layers above the sediment was reduced (Kühn *et al.*, 2015; Mordecai *et al.*, 2011). Ingestion of litter is widely spread among marine fauna, including filter-feeding organisms (Galgani, 2015). Shellfish can capture microplastics, small plastic particles as a result of plastic degradation, by their filtering apparatus (Lusher, 2015; Sussarellu *et al.*, 2016). Thus, CWCs may trap these microplastics in a similar way and suffer physiological consequences. Except for the ingestion of the pieces of plastic itself, chemicals released by the degradation process may also contaminate filter-feeders and their predators (Galgani, 2015).

However, litter could provide new substrate and therefore enhance colonization of litter by sessile organisms (Galgani, 2015). Multiple corals and non-corals, including *L. pertusa* and *M. oculata*, were observed to be settled on plastics, fishing gear and other litter items (Mordecai *et al.*, 2011; Ramirez-Llodra *et al.*, 2013). Even though the settlement of species may increase the

local diversity (Mordecai *et al.*, 2011), this could have potential negative effects on the predation and competition for space and food by non-natural changes in the species composition (Bergmann and Klages, 2012).

Even though it is clear that litter impacts marine organisms, the exact extent of its impact and the litter distribution remains elusive, with more than 95% of the deep sea remaining unexplored. Despite recent studies reporting the physical damage and death of CWC colonies and discussing the potential negative effects on biotic interactions in a community as well as suggesting significant adverse effects on the physiology of several species (e.g. Kühn *et al.*, 2015; Sussarellu *et al.*, 2016), the precise impact on a population and organism level remains largely unknown (Kühn *et al.*, 2015).

3.2. Fisheries

3.2.1. Bottom trawling

After the 1960s the fisheries moved towards deeper waters, due to the depletion of fish or regulations in shallower waters as well as the development of better fishing gear (Ramirez-Llodra *et al.*, 2011). Trawling forms probably the highest threat to CWCs (Benn *et al.*, 2010). The spatial extent of trawled area for the Hatton and Rockall Bank region was estimated using data from the vessel monitoring systems (VMS) of 28 vessels for the year 2005 (Benn *et al.*, 2010). The VMS is a satellite based monitoring system, providing data on location, course and speed of fishing vessels to the fisheries authorities at regular intervals. Benn *et al.* (2010) estimated a minimum trawled area of 548 km² and a maximum trawled area of 13,920 km² (overlapping tracks were merged). This area may be underestimated, since not all vessels fishing in this region were included in the study (Benn *et al.*, 2010). However, trawling vessels do target specific areas of the Hatton – Rockall region (Fig. 10) (Benn *et al.*, 2010). At the moment, Hatton Bank is protected by a closure to all bottom gear that was put in place in 2006 (Durán Muñoz and Sayago-Gil, 2011).

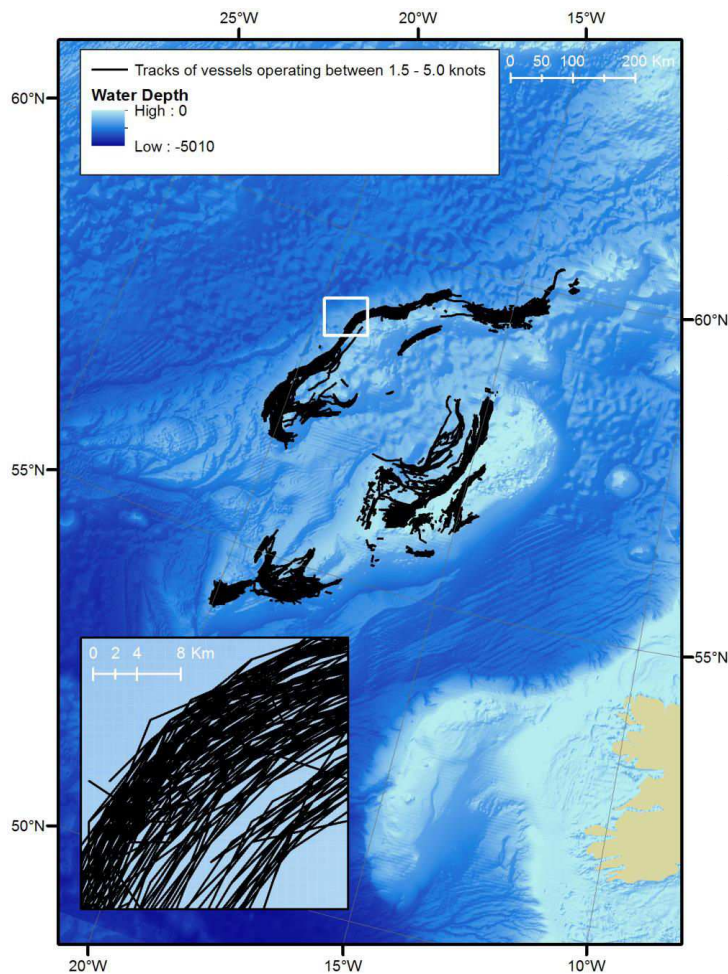


Figure 10: Bottom trawling paths at the Hatton-Rockall Bank area. Tracks of vessels operating between 1.5 and 5.0 knots during 2005. Reproduced from Benn *et al.* (2010).

In the history, the fishing industry avoided areas dominated by sponges and corals, because the fishermen risked ripping or losing their fishing gear, but the development of better and stronger nets these risks decreased (Roberts *et al.*, 2009). Interactions between CWCs and the trawling industry are already known since the early 20th century. Joubin (1922) reported that CWCs damaged trawling gear. Within his work, it was mentioned that fishermen sometimes brought up 6 tonnes of corals in a single haul. Due to the shoaling behaviour of certain species above or in coral reefs and sponge grounds, it is interesting for fishermen to fish in or on the border of these areas. Orange roughy (*Hoplostethus atlanticus*) and oreos (*Oreosomatidae*), among other fish species, were seen to aggregate above coral reefs and seamounts (Koslow, 2007). Orange roughy was also observed to aggregate in submarine canyons and these aggregations could be very large including more than 4000 individuals (Lorance *et al.*, 2002; Uiblein *et al.*, 2003). However, trawling can damage coral reefs in a severe and potentially permanent way (Fig. 11). Fosså *et al.* (2002) estimated that 30 to 50% of the *L. pertusa* reefs, with a total estimated area between 1528 and 1815 km² along the Norwegian margin, are damaged or impacted by bottom trawling. The damage of *L. pertusa* reefs off Norway is an example of impact by the removal of the habitat engineers. This also has been observed in other regions: in trawled areas west of Ireland, the structuring species *L. pertusa* was completely destroyed into pieces by trawls, while *L. pertusa* on untrawled areas was forming a live three-dimensional structure (Hall-Spencer *et al.*, 2002); *S. variabilis* thickets on seamounts off the coast of Tasmania (Australia) were destroyed and their bottom cover was reduced by two orders of magnitudes (Althaus *et al.*,

2009); bare hard substratum or coral rubble covered the trawled Tasmanian seamounts instead of a live coral thicket of *S. variabilis* (Koslow *et al.*, 2001), similar to the trawled seamounts Graveyard and Morgue off New Zealand (Clark and Rowden, 2009).



Figure 11: Trawl mark observed by a Remotely Operated Vehicle at 220 m water depth at Sørmannsneset off Norway. Only broken pieces of *L. pertusa* are visible. Reproduced from Fosså *et al.* (2002).

In addition to the removal of engineering species, other effects of trawling exist (reviewed by Clark *et al.*, 2016). Trawling could cause changes in abundance and biomass as well as in community structure. The biomass, mainly composed by *S. variabilis*, on untrawled Australian seamounts was seven times higher than the biomass in dredge samples from trawled seamounts (Koslow *et al.*, 2001). Further, changes in species compositions were also observed for these Australian seamounts: live *S. variabilis* characterised the unfished or lightly trawled seamounts, whereas the species composition of shallow heavily fished seamounts was not characterised by a specific species (Koslow *et al.*, 2001). Clark and Rowden (2009) also observed clear and significant differences in macro-invertebrate species composition of trawled and untrawled seamounts. Changes in community structure could also occur by the removal of large predators such as fish, but also smaller epibenthic fauna, e.g. echinoderms (Gage *et al.*, 2005) and may help certain species to become dominant and therefore a change in diversity and composition of the community could happen. Indeed, smaller scavenging and predator species, e.g. the gastropods *Buccinum undatum*, *Boreotrophon clathratus*, *Neptunea despecta* and *Arrhoges occidentalis* and the bivalve *Astarte undata*, were directly associated to areas with a high trawling activity on the Flemish Cap and the Grand Bank off Canada (Murillo *et al.*, 2011). Further, trawling could cause a decrease in diversity. Species richness of macrofauna was reduced on trawled seamounts off Australia: samples of untrawled or lightly trawled seamounts contained more species than heavily fished sites (Koslow *et al.*, 2001). The diversity of the benthic megafauna community on hard and soft substrata in the Bering Sea decreased with increasing fishing activity with otter trawls (based on VMS data) (Buhl-Mortensen *et al.*, 2016). More specifically, negative relations with fishing activity were observed for sea pens including *Kophobelemnion stelliferum*, the gorgonian *P. arborea* and the solitary coral *Flabellum macandrewi* (Buhl-Mortensen *et al.*, 2016).

Besides direct interactions between trawl gear and corals, trawling can also impact cold water corals by indirect effects. Trawling causes a significant amount of sediment to be resuspended in the water column. Currents transport this resuspended sediment to corals, especially in submarine canyons as conduits for sediment transport. The effects of trawling on the sediment processes in submarine canyons is well studied in the canyons of the north-western Mediterranean Sea, especially La Fonera (or Palamós) Canyon, because of the intensive blue and red shrimp *Aristeus antennatus* fisheries in this area (Puig *et al.*, 2012). Sediment cores in La Fonera Canyon showed differences between trawled and untrawled sites (Martín *et al.*, 2014a). Within this canyon, trawling takes place between 400 and 800 m water depth. Martín *et al.* (2014a) observed that the first layer of sediment on trawled sites was denser and deposited in an earlier time period than the sediment at untrawled sites, suggesting that the sediment was eroded by trawling, whereas there was recent sediment accumulation at untrawled sites. Gravity flows occurred within the same canyon and may be induced by trawling on the canyon wall, because the flows were only observed during the working hours on working days of the week (Palanques *et al.*, 2006b). These gravity flows were measured at a depth of 1200 m at the canyon axis, suggesting that trawling induced gravity flows can be transported far from the source of trawling occurring on the flanks between 400 and 800 m depth. Furthermore, gravity flows may form nepheloid layers with a thickness of a 100 m as measured by turbidity meters (Martín *et al.*, 2014b). In Whittard Canyon (Bay of Biscay), enhanced nepheloid layers – layers with a higher turbidity than other more typical nepheloid layers in the canyon – were recorded at water depths between 640 and 2880 m (Wilson *et al.*, 2015). The authors suggested that these layers could be caused by trawling of the adjacent spurs or on the shelf edge at the head of the canyon, since the layers were present during or directly after trawling activities as shown by VMS data. Trawling can also change the seafloor relief; the canyon flanks of La Fonera Canyon were smoothed by repeatedly scraping off the seafloor by trawl doors as observed by Puig *et al.* (2012). The authors observed smoothed canyon flanks at depths shallower than 800 m on the bathymetry by their homogeneous slopes and low rugosity and these flanks corresponded exactly with the navigation tracks of trawlers. Further, trawling could change the substrate type of the seafloor decreasing substrate heterogeneity; either hard substrate is exposed by erosion or sediment is deposited, due to changes in seafloor relief, slope and hydrodynamics. The repeated resuspension of sediment favours grain-size separation, due to the differences in settling speeds that is higher for coarser sediment, such as sand. In La Fonera Canyon, changes in grain size was associated with trawling; sediments had higher sand contents on trawled sites than untrawled sites (Martín *et al.*, 2014a). On the Grande-Vasière, a part of the continental shelf of the Bay of Biscay, the 30% decrease in mud content of sediments between 1964 and 2014 was mainly caused by natural events, such as storms, but the overall yearly contribution of trawling to the sediment resuspension was in the order of 1% (Mengual *et al.*, 2016). However, the authors suggested that the sediment resuspension induced by trawling may become dominant in summer, what is the fishing season, and at higher water depths.

The recovery of a coral community from trawling is a very long process and, thus, cold-water coral habitats have a low or no resilience to trawling. The term resilience here defines the time a habitat needs to recover from the effect of a pressure, once that pressure has been reduced (La Rivière *et al.*, 2016). Repeated trawling can decrease sexual reproduction success and,

therefore, reduces the recovery rate of an area, as suggested for the Darwin Mounds (NE Atlantic), where *L. pertusa* colonies were probably not able to reach sexually viable sizes (Waller and Tyler, 2005). Male colonies of the soft-bottom dwelling gorgonian *L. sarmentosa* in the Western Mediterranean are not fertile before their size reaches 21 cm (Rossi and Gili, 2009). Even after five or ten years after trawling has ceased, recovery of seamount communities including *S. variabilis* was hard to observe (Williams *et al.*, 2010). The authors surveyed the community of three seamounts off New Zealand with a five-year period between surveys and three other seamounts off Australia with a ten-year period between surveys. In both regions, one seamount was still being trawled, on one seamount trawling had ceased and one seamount was never trawled. A clear recovery of the communities of the seamounts where trawling had ceased was not observed, but it may be possible that this time period is too short for long-lived and slow growing organisms, such as CWCs, to recover (Williams *et al.*, 2010). Living *S. variabilis* was only observed on untrawled seamounts, while exposed hard substrate covered the seamounts that had been or were still trawled. Some species were observed in higher abundances on seamounts where trawling had ceased compared to the community on never trawled seamounts, e.g. Chrysogorgiidae gorgonians and echinoids. However, the authors suggested that these species had either a higher resistance to trawling or were protected by 'hiding' in crevices or behind boulders that cannot be accessed by trawl gear. Another possibility is that these species could be the earliest stage of recolonisation of seamounts (Williams *et al.*, 2010).

Another study to the recovery of coral communities after trawling concerns the Darwin carbonate mounds in the Rockall Trough off Scotland (Huvenne *et al.*, 2016). Backscatter data showed lineation caused by trawl doors on these mounds, indicating that these mounds have a trawling history (Wheeler *et al.*, 2008). A Marine Protected Area (MPA) was designated in 2003 prohibiting all bottom contact fishing, especially trawling, and the mound area became a Special Area of Conservation under the EC habitats Directive in December 2015 (Huvenne *et al.*, 2016). The Darwin Mounds were surveyed again by a Remotely Operated Vehicle (ROV) in 2011, eight years after the fishing closure (Huvenne *et al.*, 2016). The authors concluded that there was almost no recovery of the coral community after eight years trawling had ceased. Trawl marks that were observed in the initial survey in 1998-2000, so 3 to 5 years before closure, could not be identified anymore in 2011, even though some 'fresh' marks could be observed, suggesting that some fishermen violated the closure. However, similarly as *S. variabilis* on the Australian and New Zealand seamounts, recovery of the *L. pertusa* coral community on the Darwin mounds was minimal: the mounds were still covered by dead coral fragments and live colonies were absent or sparse (Huvenne *et al.*, 2016).

The communities of three types of Hawaiian seamounts, distinguished by their trawling history (never trawled, trawling ceased in 1977 and still trawled), were compared (Baco, 2016). Trawling scars were visible on the hard substrate in seamounts that were still trawled or had been trawled. A rich cold-water coral community, including gorgonians and scleractinians, dominated the never-trawled seamounts, whereas the trawled seamounts were covered by bare substratum. The community of the seamount where trawling was ceased, showed some signs of recovery, and was composed of cnidarians, fishes and echinoderms, similarly to the never-trawled seamounts. However, differences in dominant species, diversity and abundances between the recovering communities and the never-trawled community existed.

These research studies on the recovery of CWC communities show that the resilience of these habitats is low. After 5 to 10 years, no recovery has been recorded yet and it may well be that even more than 38 years after the anthropogenic pressure has ceased, CWC communities still do not have the same status as prior to the impact. This is not surprising taking the slow growth rates of cold-water corals, of only a couple of millimetres to centimetres a year, into account (see section 2.1.1. and 2.2.1. of this chapter). Furthermore, recolonisation may not take place within the time period of observations, e.g. 5 years, or other species may benefit from the available substratum and recolonise areas faster, for example echinoids on Australian seamounts where trawling had ceased. The low resilience, together with a low resistance and a low ability to recolonise, results into a high sensitivity of CWCs to trawling (La Rivière *et al.*, 2016).

3.2.2. Long-lining

Bottom long-lines and other passive fishing gear can also impact CWCs, but in a lesser extent compared to trawling (Fabri *et al.*, 2014; Fosså *et al.*, 2002; Pham *et al.*, 2014b). CWCs are still abundant and healthy around the Azores archipelago that is subjected to an intensive longline fishery industry (Pham *et al.*, 2014a), whereas trawling damages can be severe. However, impacts of longlines were recorded: CWCs, such as *M. oculata*, were seen to be entangled in lost long-lines (Fabri *et al.*, 2014; Grehan *et al.*, 2005; Kühn *et al.*, 2015; Orejas *et al.*, 2009) and they have been frequently reported as by-catch (Braga-Henriques *et al.*, 2013; Durán Muñoz *et al.*, 2011; Grehan *et al.*, 2005). Lost long-lines and nets can continue to fish what is called ghost-fishing, impacting especially the fish and crustacean communities, but can cause damage to CWCs (Grehan *et al.*, 2005; Ramirez-Llodra *et al.*, 2011). Longlines were recorded to move along the seafloor at Hatton Bank (Durán Muñoz *et al.*, 2011). Even though interactions between longline gear and CWCs were observed, little is known about the extent of the impact of longlining on CWCs and this may be difficult to establish. In Cap de Creus Canyon (Mediterranean), there was no clear relationship between the distribution of longlines and coral density and local variations existed (Orejas *et al.*, 2009). Furthermore, the amount of impact depends also on the fishing intensity and the spatial distribution of this type of fishing (Ramirez-Llodra *et al.*, 2011) as well as the CWC species itself as it was found that organisms with a complex morphology, e.g. reef-building scleractinians, are more likely to become by-catch and decline in abundance (Pham *et al.*, 2014a).

3.3. Oil and gas industry

The oil and gas industry is exploiting the deep sea and a drill exists at 3051 m water depth in the Gulf of Mexico (Davies *et al.*, 2007; Ramirez-Llodra *et al.*, 2011; Roberts *et al.*, 2009). The oil and gas industry can have a range of potential impacts on CWCs, of which the discharge of a mix of drill cuttings and drill mud is probably the greatest threat (Roberts *et al.*, 2009). Drill cuttings are broken pieces of rock (Roberts *et al.*, 2009) and drill mud are drilling water, oil or synthetic based fluids mixed with a weighting material, typically barite (BaSO₄), and additives, e.g. viscosifiers and emulsifiers (Bakke *et al.*, 2013).

Drill cuttings could smother cold-waters corals. Aquarium experiments showed that drill cuttings smothered *L. pertusa* and caused a significantly higher mortality of the polyps that were completely covered by the cuttings compared to the control where coral burial did not take place (Larsson and Purser, 2011). Large particles of the drill cuttings sink quickly and are deposited close to the oil well (Neff, 2005), but smaller particles from the drill cuttings and mud could affect a larger area. Barite crystals originating from an oil well in an area of *L. pertusa* reefs off Norway (Traena Deep) were found at a distance of four km from the well, but the discharges were small-scaled and negative effects on the CWCs were limited (Lepland and Mortensen, 2008). Jones *et al.* (2007) investigated the megafaunal community near a drilling well in the Faroe-Shetland channel and concluded that the megafaunal assemblages were disturbed the most in an area within approximately 50 m of the well; decreased abundances of megafauna were measured as a result of smothering by drill cuttings. Although drill cuttings could have negative effects around a 100 m from the source, this was variable between locations, of which the current regime and the nature of the drilling was not the same (Jones *et al.*, 2007). The communities in this study did not include corals, but was mainly composed of filter/suspension-feeding sponges and CWCs, also filter-feeders, might be affected similarly. The currents probably diluted the impact of contaminants released by the oil and gas industry and may decrease the effects on deep-sea species further from the source (Davies *et al.*, 2007). Besides, some coral species thought to be sensitive to this kind of impact, may have some resilience (Davies *et al.*, 2007). An example can be given by the live *L. pertusa* colonies growing on oil rigs in the North Sea (Bell and Smith, 1999; Gass and Roberts, 2006). Oil spills can have impacts at a larger scale and causes the highest amount of contamination (Ramirez-Llodra *et al.*, 2011). The Deepwater Horizon oil spill began on April 10th 2010 in the Gulf of Mexico, after the explosion of safety valves (Ramirez-Llodra *et al.*, 2011). Fisher *et al.* (2014) assessed the impact of oil and/or dispersant released in the water during the oil spill on coral communities at nine sites in the Gulf of Mexico. The coral communities closer to the well were more impacted than those further from the source, but coral colonies at a distance of 22 km southeast of the well showed signs of impact (Fisher *et al.*, 2014).

3.4. Climate change

Climate change is probably the most challenging threat to cold-water corals (Roberts and Cairns, 2014), because it impacts at a global scale, whereas other threats, such as litter and the fishing industry, are more on a local scale. The level of atmospheric carbon dioxide (CO₂) has increased and causes the warming and acidification of the Oceans (Davies *et al.*, 2007; Menot *et al.*, 2010; Ramirez-Llodra *et al.*, 2011); of the total CO₂ emission in the atmosphere between 1750 and 2011, equivalent to 2040 ± 310 GtCO₂, approximately half has occurred in the last 40 years (IPCC, 2014). The warming and acidification of the oceans can have a chain of reactions that directly or indirectly impact CWCs.

In approximately forty years, from 1961 to 2003, the temperature has risen by 0.1°C and it is estimated to increase another 0.5°C in the next century (Menot *et al.*, 2010; Ramirez-Llodra *et al.*, 2011). According to the International Panel on Climate Change (IPCC), it is certain that the first 700 m of the ocean have warmed since 1971 and it is likely that the temperature of deeper

parts of the ocean (between 700 to 2000 m water depth) have increased from 1957 (IPCC, 2014). Even at depths over 3000 m this increase is likely to occur since the last two decades (IPCC, 2014). In the Bay of Biscay, particularly, models showed that the temperature of the 0 to 200 m water depth layers has increased by $\sim 0.2^{\circ}\text{C}$ per decade over a period of 40 years (1965-2004) (Michel *et al.*, 2009). *L. pertusa* and *M. oculata* as well as other coral species living in deep water could respond dramatically to temperature changes (Roberts *et al.*, 2009). Aquarium experiments showed that a deeper population (40 m) of the Mediterranean red coral *Corallium rubrum* was more sensitive to an increase of temperature than the shallower population (10 m); the former showed signs of mortality caused by increasing temperatures in an earlier time period (Torrents *et al.*, 2008). Exposure to high temperatures for a longer period of time (over 20 days) was suggested to be the reason of the mass mortality among this coral type off Marseille in the Mediterranean Sea in the summers of 1999 and 2003 (Torrents *et al.*, 2008). Although the deepest specimens of *C. rubrum* in the previous study occurred at depths of 40 m, it may be possible that corals living in much deeper waters might already be affected by a small temperature increase and after shorter time periods. Temperature increases of the seawater could potentially penetrate until 700 m water depth in many oceans, including the NE Atlantic (Barnett *et al.*, 2005) as also mentioned by the IPCC (2014).

An increasing sea water temperature can have multiple direct and indirect effects on marine organisms (Fig. 12). The increased temperature around the globe melts the polar ice caps (Davies *et al.*, 2007; IPCC, 2014; Menot *et al.*, 2010). In temperate waters, this causes an increase in density stratification of the oceans (Davies *et al.*, 2007; IPCC, 2014; Menot *et al.*, 2010) which may decrease primary productivity in surface waters and the organic matter supply to the seafloor (Chust *et al.*, 2014; Davies *et al.*, 2007; MacNeil *et al.*, 2010; Menot *et al.*, 2010). In polar regions, the primary production is expected to increase due to the reduction of the ice sheet (Chust *et al.*, 2014; IPCC, 2014; MacNeil *et al.*, 2010). A geographical (poleward) or bathymetrical (to deeper waters) shift of organisms is an effect of global warming (IPCC, 2014; Menot *et al.*, 2010) that can be related with changes in distribution of surface productivity (Davies *et al.*, 2007). These shifts can lead to a community turnover in temperate areas, with the arrival and increased dominance of warm-water species and the departure of cold-water species (MacNeil *et al.*, 2010). Species replacement and decreased coral cover has been observed in tropical coral reefs as a result of ocean warming (IPCC, 2014) and cold-water coral reefs may react in a similar way.

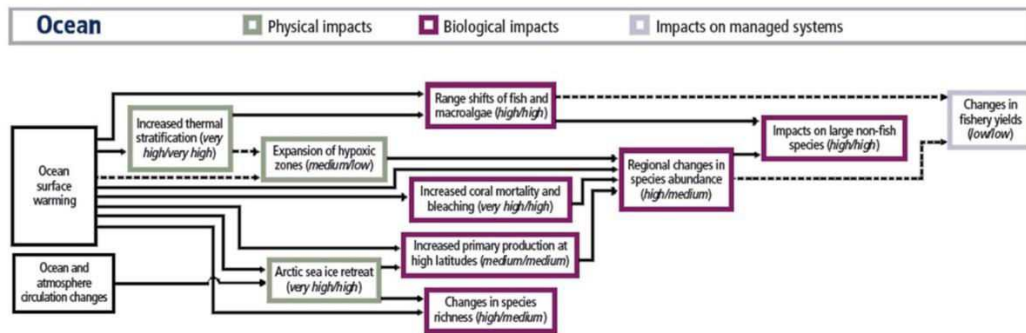


Figure 12: Major (solid lines) and minor (dashed lines) effects of climate change on the ocean. The effects of ocean acidification are similar to the effects of global warming as indicated by initial evidence. The text between brackets indicated the confidence in detection/confidence in attribution. Reproduced from IPCC (2014).

The ocean is a natural sink for CO₂, but it absorbed already at least 30% of the CO₂ emitted by human activities between 1750 and 2011 (IPCC, 2014; Ramirez-Llodra *et al.*, 2011). The increasing level of CO₂ in the sea water reacts with the water by creating carbonic acid (H₂CO₃), lowering the pH with oceans becoming more acidic as a consequence (Davies *et al.*, 2007; Menot *et al.*, 2010). The average pH of the ocean has declined by 0.1 units since pre-industrial times and is predicted to decrease by another 0.3-0.7 units under the IPCC IS92a scenario as shown by observations and models (Davies *et al.*, 2007 and references herein). The IPCC has set up six scenarios of future emission of gasses involved in climate changes, e.g. CO₂ (IPCC, 2000). The IPCC IS92a scenario is the ‘Business-as-usual’ scenario with few or no steps taken to limit CO₂ emission (IPCC, 2000). In a later stage, the IPCC has developed four Representative Concentration Pathways (RCPs) that describe pathways of greenhouse gas emissions, including CO₂, as well as atmospheric concentrations, air pollutant emissions and land use (IPCC, 2014). These pathways include a stringent mitigation scenario (RCP2.6), two intermediate scenarios (RCP4.5 and RCP6.0) and one scenario with a very high greenhouse gas emission (RCP8.5) (IPCC, 2014). It is predicted that a scenario without additional efforts to constrain emission of greenhouse gases, so similar to the IS92a scenario, should range between RCP6.0 and RCP8.5 and, thus, a CO₂-eq concentration would be higher than 720 ppm (IPCC, 2014; Fig. 13).

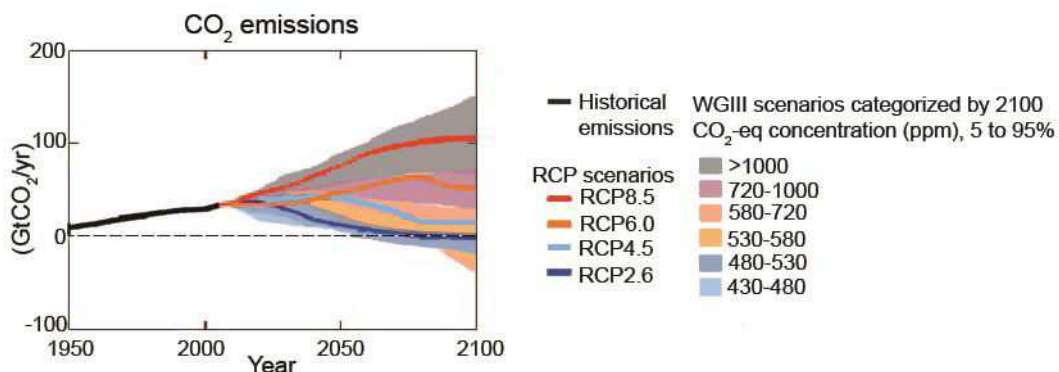


Figure 13: Carbon dioxide (CO₂) emission for the different Representative Concentration Pathways (RCP) and the associated scenario categories used in the WGIII (Working Group III). The WGIII scenario categories summarize the wide range of emission scenarios published in scientific literature and are defined based on the total CO₂-equivalent concentrations (in ppm) in 2100. Reproduced from IPCC (2014).

Shallow-water organisms are the first to be affected by ocean acidification; the higher levels of CO₂ increase the photosynthetic rate of some phytoplankton species that may have impact on growth and composition of phytoplankton communities on the long-term (Davies *et al.*, 2007). However, organisms in deeper waters, such as cold-water corals, might also be affected with detrimental effects on the species itself as well as on the biogeography. Even though *L. pertusa* has the ability to physiologically acclimate to increased CO₂ and temperature, the aragonite crystal organisation in its skeleton changes as a response to increased acidification, causing a weaker skeleton (Hennige *et al.*, 2015). The question remains whether the acclimation of *L. pertusa* reefs can continue at a rate necessary for the reef to develop and grow or that a change in energy allocation to other important processes, such as reproduction, have negative effects on the strength of the skeleton (Hennige *et al.*, 2015) and, therefore, the existence of reefs. A weaker skeleton is more susceptible to abrasion and bioeroders, such as sponges.

On a larger level, increased CO₂ causes the so-called aragonite and calcite saturation horizons, i.e. the water depth where the sea water becomes unsaturated with respect of aragonite and calcite, to shallow (Davies *et al.*, 2007; Hennige *et al.*, 2015). Octocorals, antipatharians and certain species of scleractinians (*L. pertusa*, *M. oculata*, *S. variabilis*, *E. rostrata* and *G. dumosa* and multiple solitary scleractinian species) are observed in sea water that is saturated of aragonite and calcite (Davies and Guinotte, 2011; Davies *et al.*, 2008; Guinotte and Davies, 2014; Yesson *et al.*, 2012). CWCs use inorganic dissolved carbon and calcium carbonate (CaCO₃) in the form of calcite or aragonite to build their skeleton. In calcium carbonate saturated sea water, there is an equilibrium of dissolved CO₂, bicarbonate ions (HCO₃²⁻) and carbonate ions (CO₃²⁻). However, in undersaturated waters in respect to carbonate, this equilibrium is shifted and as result calcium carbonate will dissolve (Roberts *et al.*, 2009), thus meaning that the skeleton of CWCs will dissolve. The aragonite and calcite saturation horizons already shoaled by 50 to 100 m in the Pacific Ocean (Roberts and Cairns, 2014) and are shallower compared to the NE Atlantic Ocean. This is reflected by the distribution of cold-water corals in the Pacific Ocean (Davies *et al.*, 2007; Ramirez-Llodra *et al.*, 2011), where communities are dominated by octocorals and hydrocorals, instead of reef-forming scleractinians (Davies *et al.*, 2007). CWCs that are distributed at relative deeper depths may disappear; it is expected that deep populations of *D. dianthus* off New Zealand will disappear due to the shallowing of the aragonite and calcite saturation horizons combined with their limited vertical larval dispersal (Miller *et al.*, 2011).

Besides cold-water corals, other calcifying organisms, such as foraminifera, molluscs and echinoids, will be affected by ocean acidification (Menot *et al.*, 2010; Ramirez-Llodra *et al.*, 2011).

4. Conservation

Cold-water coral habitats are targets for conservation, because they are long-lived and fragile. Furthermore, they have important functions to other organisms, e.g. shelter, reproduction and nursery grounds and feeding areas. In recent decades, several international initiatives have suggested that CWCs are indeed susceptible to human activities that resulted in multiple

national and international measures to protect these ecosystems. The high biodiversity that characterise CWC habitats, especially coral reefs plays a key role in the conservation of cold-water coral habitats (EC, 2008; UNGA, 2006). The most important initiatives are probably those of the UNGA, the OSPAR commission, the Habitats Directive, the Marine Strategy Framework Directive and the Convention on Biological Diversity (CBD).

The term “vulnerable marine ecosystems” (VME) is often used to refer to cold-water coral habitats in a conservation context. The term comes from the sustainable fisheries resolutions of the General Assembly of the United Nations (UNGA). These resolutions were set up to prevent adverse impacts on VMEs, including CWCs, caused by human activities, especially by bottom trawling, and therefore calls upon States and/or local, regional and international fisheries organizations, such as the Food and Agriculture Organizations (FAO) of the UN, to set up programmes and fisheries regulations for the protection of VMEs (see UNGA, 2004, 2006, 2009). A VME is defined as “any deep-sea ecosystem that has very high vulnerability to one or more kinds of fishing activity” (FAO, 2007). VMEs can be identified by characteristics on their uniqueness or rarity, functional significance for the habitat, fragility, life-history traits, e.g. slow growth, long-lived and the age of maturity, and on the structural complexity (FAO, 2009). The UNGA recognises the work done by the FAO in providing recommendations for the management of deep-sea fisheries to aim for the conservation and sustainability of living resources and to prevent significant impact on VMEs (UNGA, 2004, 2006, 2009). One of the means of the FAO to provide these recommendations is via the International guidelines for the management of deep-sea fisheries in the High Seas (FAO, 2009). In addition to CWCs, hydrothermal vent and seamount communities, should benefit from conservation measures (UNGA, 2004, 2006). The UNGA also states the necessity for the identification of VMEs, the determination of the impact of bottom trawling on these VMEs and to cease bottom trawling in areas where VMEs occur (UNGA, 2006). In a following resolution, the UNGA called upon States and fisheries organizations to make the assessments of bottom fishing’s adverse impacts on VMEs publicly available (UNGA, 2009).

The Oslo-Paris Convention (OSPAR) is an agreement between 15 European countries and the European Commission to assess the species and habitats that need protection and to prevent impact of human activities on these species and habitats (Annex V; OSPAR, 2008). With this goal, OSPAR has set up a list of “Threatened and/or Declining Species and Habitats” in 2008 (OSPAR, 2008). These species and habitats are defined on several criteria that consider the global and regional importance, rarity, sensitivity and status of decline (OSPAR, 2003). A sixth criterion for habitat is its ecological significance and for species whether it is a key-stone species or not (OSPAR, 2003). Coral gardens, *Lophelia pertusa* reefs and sea pen and burrowing megafaunal communities, but also sponge aggregations, are deep-sea habitats that are listed by OSPAR as threatened and/or declining. Listed geological features include carbonate mounds, seamounts and oceanic ridges with hydrothermal vents. Further, several shark species, such as *Centrophorus* spp. (gulper sharks), and other fish species, e.g. orange roughy, commonly observed in the deep sea are also listed, although the OSPAR commission is not implemented in fisheries management.

The Habitats Directive, or the Council Directive 92/43/EEC on the Conservation of natural habitats and of wild fauna and flora (EEC, 1992) is also a European initiative. It protects over 1000 European species other than birds (they have their own Birds Directive) and over 200

habitats, both on land and in water, which are considered to be endangered, vulnerable, rare and/or endemic, within Europe (EEC, 1992). Annex I of the Habitats Directive contains natural habitats that are of interest to protect and are selected on several criteria, including the degree of representativity of the habitat, the area covered by this habitat and the degree of conservation (EEC, 1992). Annexes II to V contain species that are considered to be vulnerable. Criteria for species are size and density of the population, degree of conservation and degree of isolation of the population (EEC, 1992). Reef (1170) is part of the Habitats Directive Annex I and can be of a biogenic or geogenic origin. Reefs are considered as “hard compact substrate, i.e. rock, boulder and cobbles, on solid and soft bottoms, which arise from the seafloor in the sublittoral (including deep-water areas such as bathyal) and littoral zone” and “may support a zonation of benthic communities of algae and animal species as well as concretions and corallogenic concretions” (European Commission, 2013). Cold-water corals are considered as reef-building species in many marine regions, e.g. North Atlantic Ocean and the Mediterranean Sea, and may be indicated by the species name, e.g. *P. clavata* “forests” and *M. oculata* and *L. pertusa* communities (European Commission, 2013). Several non-reef forming species, such as sponges, anthozoans and barnacles, are also falling under the 1170 reef definition (European Commission, 2013). Because the 1170 Reef habitats under the Habitats Directives includes every part of the seafloor covered by hard substrate as well as topographic features, e.g. seamounts, hydrothermal vents, vertical rock walls, overhangs and horizontal ledges (European Commission, 2013), this definition is quite large.

The goal of the Marine Strategy Framework Directive (MSFD: 2008/56/EC) is also to promote a sustainable use of the seas and to conserve marine ecosystems (EC, 2008). The MSFD strives for a Good Environmental Status of EU marine waters by 2020, meaning that the ecologically diverse and dynamics oceans are clean, healthy and productive. It also includes that marine ecosystems are fully functional and resilient to human-induced environmental change; that the biodiversity of these ecosystems is maintained by preventing a decline caused by human activities and a protection of this biodiversity; and that any substances introduced by humans, e.g. litter and chemical pollutants, do not cause any harmful effects. CWC habitats can be protected under the MSFD, due to their high diversity and their sensitivity to human activities. This could be done by the integration and by setting up measurements for spatial protection of these CWC habitats by special areas of conservation or marine protected areas. A coherent and representative network of these protection measures is necessary that adequately covers the diversity of constituent ecosystems, and may involve MPAs part of the Habitats Directive or Birds Directive (EC, 2008).

The main objectives of the Convention on Biological Diversity (CBD) are the conservation of biodiversity, a sustainable use of the components of this biodiversity and the fair and equitable sharing of the benefits arising out of the utilization of genetic resources (United Nations, 1992). Under the CBD, governments need to develop management plans to identify, monitor and protect components or areas of biodiversity as well as the restoration of degraded ecosystems and the recovery of threatened species. One of the targets of the strategic plans for Biodiversity 2011-2020 under the CBD is Aichi Biodiversity target 11: it includes the conservation of 10% of the coastal and marine areas, especially areas of particular importance for biodiversity and ecosystem services, such as CWC habitats, by 2020 and would be done by an effective

management, ecological representativity and a well-connected network of marine protected areas (<https://www.cbd.int/sp/targets/rationale/target-11/>).

Even though differences in the criteria of the different initiatives exist, key-words of all initiatives are “uniqueness/rarity”, “sensitivity” and/or “vulnerability”. The sensitivity of a habitat is a combination of the resistance (tolerance to anthropogenic pressure) and resilience (time to recover from anthropogenic pressure) of this habitat (La Rivière *et al.*, 2016). The vulnerability of a habitat is usually the risk that a habitat can have to be impacted by human activities (La Rivière *et al.*, 2016). The vulnerability depends on the intensity, type, duration and spatial extent of anthropogenic impact on these species/habitats, the resistance and resilience of the species/habitats to this impact. All these habitats are in some way sensitive to human activities by the removal and/or destruction, suffocation and sedimentation of the engineering species.

The need for the protection of cold-water coral habitats, especially reefs, is high. As shown in the previous sections of this chapter, the impact of human activities on corals is large. Only a small number of deep-sea habitats are protected, focalising especially on cold-water corals and hydrothermal vents (Davies *et al.*, 2007). After identifying the species or habitat that needs to be protected, several measures can be set up to protect CWC habitats, but that depends on the initiative. One of these measurements is a fishery restricted area. Within these areas, certain types of fishing, especially bottom gears such as trawls, are temporarily or permanently prohibited to protect a species or metier (ICES, 2003). Another measurement is the “move-on rule”, based on the idea that a fishing vessel will move a certain distance from a location where VME species have been caught (Auster *et al.*, 2011). These measurements can be important for the FAO, while Marine Protected Areas could be put in place according to the OSPAR initiative, as done for the Darwin Mound closure. The Habitats Directive establishes a network of Natura 2000 sites as a measure of protection.

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Chapter 2

The French Atlantic: Bay of Biscay

Résumé français

L'Atlantique français : Le Golfe de Gascogne

Le Golfe de Gascogne fait partie de l'Atlantique nord-est. Il est bordé à l'ouest par la France, au sud par l'Espagne et au nord par la mer Celtique. La définition géologique du Golfe de Gascogne est utilisée dans cette étude et inclut les marges Celtique, Armoricaire et Aquitaine.

1. Géomorphologie

Ces marges diffèrent par leur morphologie et leur sédimentologie. La marge Celtique est limitée par l'éperon de Goban au nord et l'éperon de Berthois au sud. Cette marge est caractérisée par un grand nombre de canyons et d'éperons (Bourillet *et al.*, 2006) et influencée par les courants de marée de la Manche (Zaragosi *et al.*, 2001). Dans les canyons qui incisent cette marge, de nombreux éléments géomorphologiques tels que les falaises sont formés par l'érosion du canyon (Bourillet *et al.*, 2010). Il y a deux bassins versants – Grande-Sole et Petite-Sole – qui alimentent l'éventail Celtique (Bourillet et Lericolais, 2003).

La marge Armoricaire, limitée par l'éperon de Berthois au nord et l'éperon de Conti au sud, peut être divisée en trois zones caractérisées par des régimes de courants et de sédimentation différents. La morphologie de la marge Armoricaire du nord est très similaire à la marge Celtique, caractérisée par de nombreux canyons et éperons (Bourillet *et al.*, 2010), sous l'influence des courants de marée de la Manche (Zaragosi *et al.*, 2001). Les deux bassins versants – La Chapelle et ouest Bretagne – alimentent l'éventail Armoricain (Bourillet et Lericolais, 2003 ; Zaragosi *et al.*, 2000 ; Zaragosi *et al.*, 2001).

La marge Armoricaire centrale est caractérisée par une alternance de grands canyons et de canyons étroits, qui ne sont plus sous l'influence de la Manche (Bourillet *et al.*, 2010 ; Zaragosi *et al.*, 2001). Les deux bassins versants – sud Bretagne et Gascogne – alimentent des petits ensembles chenal-levée, au lieu d'un large éventail (Bourillet *et al.*, 2006 ; Zaragosi *et al.*, 2001).

La marge Armoricaire méridionale est caractérisée par des canyons qui sont plus lisses avec des flancs sédimentaires réguliers (Bourillet *et al.*, 2010). A l'instar des canyons de la marge Armoricaire centrale, le bassin versant, Rochebonne, n'alimente pas un éventail profond.

La dernière marge du Golfe de Gascogne français est la marge Aquitaine, limitée par l'éperon Conti au nord et le Canyon du Cap de Breton au sud (Bourillet *et al.*, 2006). Les canyons qui incisent cette marge sont beaucoup plus lisses que les canyons des deux autres marges (Bourillet *et al.*, 2006). Il y a un seul bassin versant – Les Landes – qui alimente l'éventail du Cap-Ferret (Bourillet *et al.*, 2006 ; Mulder et Zaragosi, 2006).

2. Hydrodynamisme et sédimentation

Il y a quatre masses d'eau dans le Golfe de Gascogne, qui ont une origine et une densité différentes (Durrieu de Madron *et al.*, 1999 ; Van Aken, 2000a, b). Les masses sont : (i) l'Eau Nord Est Atlantique (ENAW) entre 200 and 600 m de profondeur, (ii) les courants intermédiaires des eaux de la Méditerranée (MOW) entre 700 et 1300 m de profondeur, (iii) l'eau de la mer de Labrador (LSW) jusqu'à une profondeur de 2000 m est moins remarquable à cause d'un mélange avec le MOW, et (iv) l'eau profonde du Nord-Est Atlantique (NEADW) entre 2000 et 2600 m de profondeur.

Le régime hydrodynamique dans le Golfe de Gascogne inclut les courants de marée, les ondes internes et les courants de la pente continentale. Ces processus modifient la température, la salinité et la densité des masses d'eau et ont un rôle important dans les apports de sédiment et de nourriture.

Les courants qui suivent la pente continentale sont des courants importants dans le Golfe de Gascogne. Ils ont une direction dominante vers le nord, mais la direction peut changer selon les saisons et peut potentiellement s'inverser (Koutsikopoulos et Le Cann, 1996 ; Pingree et Le Cann, 1989 ; 1992). Les courants de la pente continentale pourraient être en relation avec les courants de marée (Pingree et Le Cann, 1990) et sont influencés localement par la topographie (Pingree et Le Cann, 1990).

Des courants de marée sont présents dans les canyons sous-marins du Golfe de Gascogne et suivent une fréquence de marée semi-diurne (par ex. Durrieu de Madron *et al.*, 1999 ; Koutsikopoulos et Le Cann, 1996 ; Mulder *et al.*, 2012 ; Pingree et Le Cann, 1989). Ils sont plus faibles dans le sud du Golfe de Gascogne, surtout sur la marge Aquitaine (Koutsikopoulos et Le Cann, 1996).

Des ondes internes ont été observées dans des canyons sous-marins du Golfe de Gascogne (Durrieu de Madron *et al.*, 1999 ; Khripounoff *et al.*, 2014 ; Mulder *et al.*, 2012 ; Pichon *et al.*, 2013 ; Pingree et Mardell, 1985). Ces phénomènes sont importants pour la resuspension du sédiment et la création de couches néphéloïdes (Durrieu de Madron *et al.*, 1999).

La sédimentation diffère dans les canyons incisant les trois marges. Les canyons au sud du Golfe de Gascogne, en particulier ceux qui incisent la marge Aquitaine, sont plus sédimentés que les canyons qui incisent la marge Celtique et la marge Armoricaïne du nord et central. Ces canyons ont un taux de sédimentation plus élevé (Mulder *et al.*, 2012 ; Schmidt *et al.*, 2014) qui peut être lié aux vitesses de courant plus faibles sur la marge Aquitaine (Mulder *et al.*, 2012).

3. Les coraux d'eau froide

3.1. La présence et la distribution

L'existence des coraux d'eau froide dans le Golfe de Gascogne est connue depuis la fin du 19^e siècle, mais les premières cartes sont publiées au début du 20^e siècle. Joubin (1922) décrivait

les scléactiniaires récifaux comme nuisibles pour les pêcheurs, parce qu'ils pouvaient déchirer les filets des chaluts ou les chaluts pouvaient y rester accrochés. Le Danois (1948) fut le premier à décrire la présence et la distribution des récifs de *Lophelia pertusa* et *Madrepora oculata*, les débris de coraux et les facies de pennatules sur la vase dans le Golfe de Gascogne français. Il a également inclut une description de la faune associée. Zibrowius (1980) a décrit 80 espèces de scléactiniaires dans l'Atlantique Nord, dont environ 35 espèces dans le Golfe de Gascogne. Reveillaud *et al.* (2008) ont compilé des données historiques, en incluant les travaux de Joubin (1922), Le Danois (1948) et Zibrowius (1980), et des nouvelles données, pour donner une vue d'ensemble des observations de 34 espèces de scléactiniaires entre 10 et 5000 m de profondeur. La première étude qui a acquis des données sur images avec un ROV est celle de De Mol *et al.* (2011). Ces auteurs ont visité deux canyons du Golfe de Gascogne et ont observé des facies à scléactiniaires avec des densités différentes, variant entre des scléactiniaires éparses et des facies scléactiniaires vivants et denses.

Hors ZEE française, des coraux profonds ont également été décrits dans des canyons aux extrémités septentrionales et méridionales du golfe de Gascogne. Les Canyons de Whittard et des South-West Approaches, au nord du Golfe de Gascogne, sont probablement les canyons les plus étudiés dans cette région. Des habitats coralliens, construit par des scléactiniaires, des coraux mous, incluant les gorgones, et des pennatules ont été observés dans ces canyons (Davies *et al.*, 2014 ; Howell *et al.*, 2010 ; Huvenne *et al.*, 2011 ; Morris *et al.*, 2013 ; Robert *et al.*, 2015).

Dans le Golfe de Gascogne espagnol, des espèces de scléactiniaires ont été récoltées et identifiées dans le système du Canyon d'Aviles (Altuna, 2013 ; Altuna et Ríos, 2014). En outre, des facies à scléactiniaires ont été observés dans le Canyon de La Gavierra qui fait partie du même système de canyons (Sánchez *et al.*, 2014).

La distribution des scléactiniaires récifaux est contrôlée par des périodes glaciaires et ses oscillations. Le Golfe de Gascogne supporte une présence continue de *L. pertusa* et *M. oculata* depuis les dernière 4,5 ka, probablement même depuis 7 ka, comme indiqué par des déterminations d'âge (De Mol *et al.*, 2011 ; Frank *et al.*, 2011), mais le développement des récifs coralliens a varié (Frank *et al.*, 2011). Il existe un gradient latitudinal de *L. pertusa* et *M. oculata* avec une dominance de *L. pertusa* dans le nord de l'Atlantique Nord et une dominance de *M. oculata* dans le Golfe de Gascogne et la Méditerranée (Arnaud-Haond *et al.*, 2015).

3.2. La communauté faunistique

La plupart des communautés étudiés est associée à *L. pertusa* et/ou *M. oculata*. Ils sont décrits par les espèces dominantes, les substrats et la profondeur à partir des données acquises par chalutage (Le Danois, 1948) ou des images (De Mol *et al.*, 2011 ; Huvenne *et al.*, 2010 ; Sánchez *et al.*, 2014). Les méthodes statistiques sont peu utilisées pour déterminer les communautés faunistiques, à quelques exceptions près (Howell *et al.*, 2010 ; Davies *et al.*, 2014).

Le Danois (1948) a rapporté que la faune associée à *L. pertusa* et *M. oculata* inclus le scléactiniaire solitaire *D. dianthus*, des hydrozoaires, des gorgones, le corail champignon du

genre *Anthomastus*, des éponges, des bryozoaires, des annélides (dont le symbiote des scléactiniaires récifaux *Eunice floridana*, qui est actuellement connu comme *Eunice norvegica*), des cirripèdes, des ophiures, des comatules, des bivalves, des crustacés et des poissons.

Des études récentes ont élargi cette liste avec l'éponge du genre *Hexadella*, des huîtres de l'espèce *Neopycnodonte zibrowii*, des bivalves du genre *Acesta*, des cérianthes, des zoanthaires, des actiniaires, des crinoïdes et comatules, des astéroïdes, des échinoïdes, des brachiopodes, des ascidies, et d'autres espèces de crustacés et de poissons (Davies *et al.*, 2014 ; De Mol *et al.*, 2011 ; Howell *et al.*, 2010 ; Huvenne *et al.*, 2011 ; Sánchez *et al.*, 2014).

Des taxons associés aux jardins de pennatule de l'espèce *K. stelliferum* incluent des cérianthes, des ophiures, dont *Ophiactis balli*, des crinoïdes et comatules, dont *Pentametrocrinus atlanticus*, une anémone de la famille de Halcampoidae et le corail bambou du genre *Acanella* (Davies *et al.*, 2014 ; Howell *et al.*, 2010).

La diversité associée aux habitats de *L. pertusa*/*M. oculata* est plus élevée que celle des habitats dominés par le substrat meuble (Davies *et al.*, 2014 ; Robert *et al.*, 2015).

3.3. Les conditions environnementales et la réponse au changement climatique

La distribution des coraux d'eau froide pourrait être principalement conditionnée par la nature du substrat, la topographie et l'hydrologie. La plupart des coraux nécessite un substrat dur, néanmoins les pennatules et certaines espèces de gorgones et d'antipathaires sont inféodées aux substrats meubles (Roberts *et al.*, 2009 ; Wagner *et al.*, 2012 ; Williams, 2011). La pente est importante également. *L. pertusa*, *Solenosmilia variabilis* et plusieurs espèces de gorgones sont observées sur les falaises et surplombs dans le canyon de Whittard (Huvenne *et al.*, 2011 ; Morris *et al.*, 2013) ou dans des zones escarpées des canyons de Penmarc'h et de Guilvinec (De Mol *et al.*, 2011).

Dans les canyons de Penmarc'h et Guilvinec, les débris de coraux sont moins profonds (250-350 m) et plus anciens (7.4-9.1 ka) que les colonies vivantes (350-950 m ; 1.2-2.3 ka) (De Mol *et al.*, 2011). Ces patrons de distribution bathymétrique et d'âge suggèrent une migration des coraux le long de la pente continentale qui pourrait s'expliquer par l'augmentation du niveau de la mer et le réchauffement des eaux de surface depuis le dernier maximum glaciaire, il y a 11.5 ka (De Mol *et al.*, 2011).

Le réchauffement climatique actuel en modifiant la température et la circulation océanique pourrait également affecter la dispersion et la connectivité des organismes (Lett *et al.*, 2010). Les modèles de dispersion des invertébrés côtiers du Golfe de Gascogne ont montré que l'augmentation de température de l'eau aurait pour conséquence de modifier la période de reproduction et la durée de stades larvaires (Ayata *et al.*, 2010).

La circulation océanique pourrait être affectée par une modification des champs de pressions atmosphériques induite par le réchauffement climatique (Pingree and Garcia-Soto, 2014). Les conséquences sont potentiellement multiples sur la saisonnalité des floraisons phytoplanctoniques ainsi que la qualité et la quantité de la production primaire

phytoplanctonique qui peuvent déterminer les périodes de reproduction et plus généralement l'état physiologique des coraux profonds (Brooke and Järnegren, 2013 ; Chust *et al.*, 2014 ; Harrison, 2011 ; Pingree and Gracia-Soto, 2014).

Au niveau de la distribution des organismes, le changement climatique causerait un déplacement de ces organismes plus profond ou plus nord. Ce décalage de la distribution également concerne les coraux d'eau froide. Cependant, les coraux d'eau froide ne pourraient pas se déplacer plus profond à cause des horizons de saturations d'aragonite et calcite qui seront beaucoup moins profond. Un déplacement aux latitudes hautes est possible, mais pourrait avoir des conséquences également. En ce moment, il y a un gradient des occurrences de *L. pertusa* au nord de l'Atlantique et de *M. oculata* au Golfe de Gascogne et le Méditerranée (Arnaud *et al.*, 2015). Si la distribution change au nord, *M. oculata*, plus tolérant à la température plus élevée, gagne du terrain, tandis que la distribution de *L. pertusa* décline parce que cette espèce est arrivée à sa limite la plus nord. Au contraire, ce déplacement au nord pourrait être évité à cause de vitesse de changement de température, couplé avec l'acidification de l'océan, les changements de la circulation et des provisions de nourriture, et l'occurrence de chalutage profonds (Frank *et al.*, 2011).

La pêche, surtout le chalutage de fond, pourrait affecter les coraux d'eau froide également. Ça pourrait contribuer à l'explication de la distribution de débris de coraux et des récifs vivants observée par De Mol *et al.* (2011). Le débris est trouvé aux zones moins profondes et avec une topographie plus lisse et qui sont plus accessible au chalut, ainsi que les zones de coraux vivants observée plus profond sont dans une zone avec une topographie plus abrupte et par conséquent moins accessible au chalut. Au contraire, les canyons sous-marins ne sont pas complètement libres d'impact anthropiques (Fernandez-Arcaya *et al.*, 2017 ; Huvenne *et al.*, 2011).

The French Atlantic: Bay of Biscay

The Bay of Biscay is part of the Atlantic Ocean and is located in the north-eastern zone of this Ocean. France is located on the east and Spain on the south of this basin. The border of the Bay of Biscay in the north differs; hydrological speaking, a line from the Penmarc'h Point in France to Cape Oriegal in Spain is the boundary between the Bay of Biscay and the Celtic Sea according to the International Hydrographic Organisation (Fig. 1). However, geological speaking, the Bay of Biscay extents from the Goban spur in the north to the Iberian margin off Spain (Fig. 1) (Bourillet *et al.*, 2006). The geological definition of the Bay of Biscay was chosen in the framework of this study.

1. Morphology

The Bay of Biscay is a passive margin, originating from erosion and deposition processes (Zaragosi *et al.*, 2000) and is incised by more than a hundred canyons (Bourillet *et al.*, 2006). It can be divided into five parts: the Celtic, Armorican and Aquitaine margins off France (Zaragosi *et al.*, 2000) and the Cantabrian and Galician margins off Spain (Sibuet *et al.*, 2004). The study area in this study is limited to part of the Celtic margin, the Armorican and Aquitaine margins and will be described in more detail afterwards.

The **Celtic margin** is limited by the Goban spur (north) and the Berthois spur (south) (Bourillet *et al.*, 2006). Many submarine canyons are incising this part of the margin (Bourillet *et al.*, 2006). Within the canyons, multiple geomorphic features, such as cliffs, exist that are formed by erosion in the head of the canyons (Bourillet *et al.*, 2010). Even though the continental shelf is wide (more than 250 km), the canyons are under the influence of tidal currents of the English Channel (Zaragosi *et al.*, 2001). They are linked with the drainage basins of rivers, such as the Seine, via the Channel paleoriver (Bourillet *et al.*, 2003). During low sea level periods, it was probably also linked to other rivers, such as the Rhine and the Thames (Bourillet and Lericolais, 2003). The Grande-Sole and Petite-Sole drainage systems are located on this margin feeding into the Celtic deep-sea fan via Whittard and Blackmud Canyons (Bourillet and Lericolais, 2003). The Celtic deep-sea fan is a mature fan that is rich of mud and sand, similar to the Armorican margin (Zaragosi *et al.*, 2000; Zaragosi *et al.*, 2001). The recent (<2000 yr BP) layers of sand in the middle and lower part of the fan, suggest that there was an episodic turbidite supply originating from the Holocene (Bourillet *et al.*, 2003; Zaragosi *et al.*, 2001). Sandbanks are located on the continental shelf in less than 10 km from the shelf break (Bourillet *et al.*, 2006; Zaragosi *et al.*, 2001) causing sand to enter the canyons of the Celtic Margin (Zaragosi *et al.*, 2000).

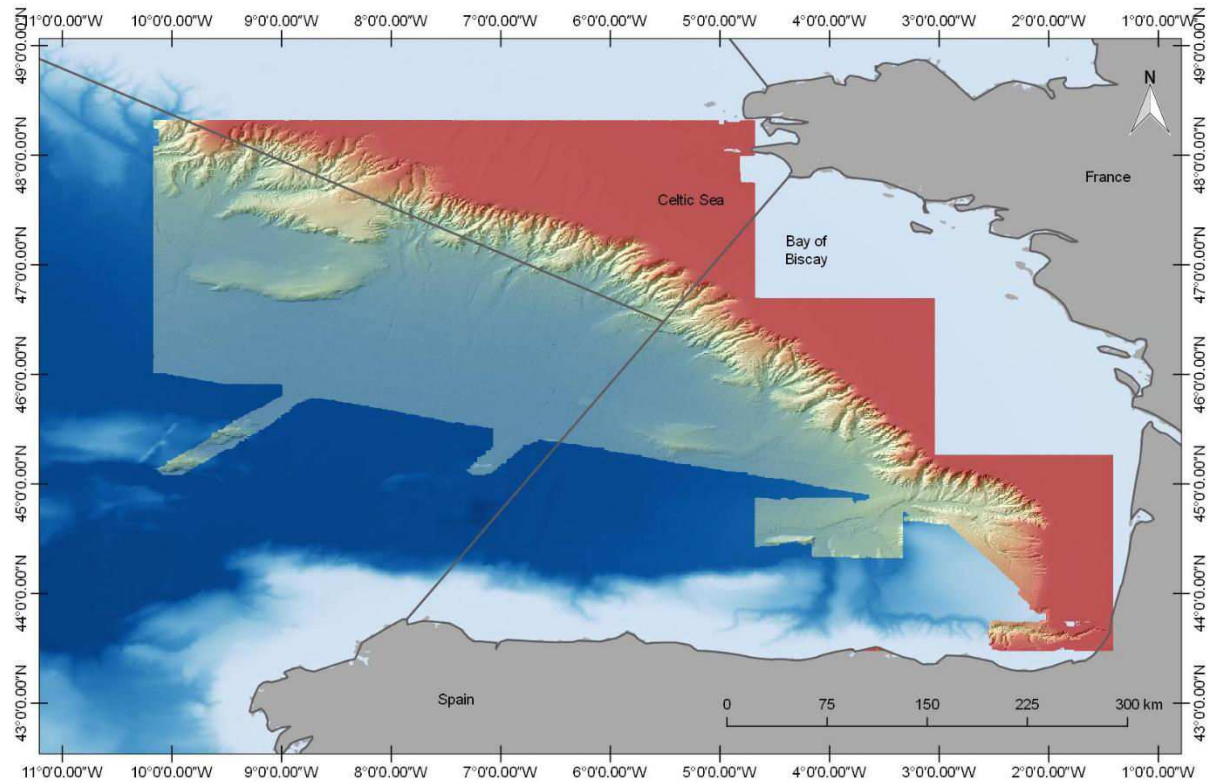


Figure 1: A representation of the Bay of Biscay. The hydrographical boundary is indicated by the grey line, dividing the basin into the Celtic Sea (above the line) and the Bay of Biscay (below the line). However, all the bathymetry in the rainbow colour is part of the Bay of Biscay, geologically defined. Two resolutions of bathymetry are used in this figure: (i) the rainbow coloured bathymetry is from Ifremer and has a resolution of 100 m; (ii) the blue bathymetry is from the GEBCO database and has a resolution of 30' arc seconds.

The **Armorican margin**, limited by the Berthois spur in the north and the Conti spur in the south, can be divided into three zones, depending on the current and sedimentation regimes (Bourillet *et al.*, 2006). The **northern Armorican margin** is similar to the Celtic margin, thus, characterised by multiple canyons and spurs, including cliffs (Bourillet *et al.*, 2010). These canyons are under the influence of tidal currents of the English Channel (Zaragosi *et al.*, 2001). The continental shelf, measuring up to 200 km wide, is slightly smaller than the shelf of the Celtic margin (Bourillet *et al.*, 2006). This part of the Armorican margins has two drainage systems – Chappelle and West Brittany – that feed into the Armorican deep-sea fan (Bourillet and Lericolais, 2003; Zaragosi *et al.*, 2000; Zaragosi *et al.*, 2001). The northern Armorican margin shares sedimentation characteristics with the Celtic margin. The main difference between the turbidity systems of these margins is that the episodic turbidity currents on the Armorican margin occurred earlier (Pleistocene-Holocene boundary; 10000 yr BP) than the turbidites on the Celtic Margin (7000 yr BP) (Auffret *et al.*, 2003; Bourillet *et al.*, 2003; Zaragosi *et al.*, 2001). Sandbanks are also present on the continental shelf of this part of the margin (Bourillet *et al.*, 2006).

The **central Armorican margin** distinguishes itself from the northern part because it is not under the influence of the English Channel anymore and it is characterised by an alternation of large and narrow canyons formed in different stages of development (Bourillet *et al.*, 2010; Zaragosi *et al.*, 2001). There are two drainage systems – South Brittany and Gascogne – that

are both feeding into small channel-levee complexes, instead of a significant deep-sea fan such as the Celtic and Armorican sea-fans (Bourillet *et al.*, 2006; Zaragosi *et al.*, 2001).

The canyons incising the **southern Armorican margin** are much smoother than the other parts of the same margin. The flanks are regular and sedimentary and geomorphological features are absent or scarce (Bourillet *et al.*, 2010). The thalwegs of the canyons are continuous with sloping banks (Bourillet *et al.*, 2010). There is one drainage system, Rochebonne, which does not feed into a deep-sea fan, similar to the drainage systems on the central Armorican margin (Bourillet *et al.*, 2006).

The **Aquitaine margin** is the third margin of the Bay of Biscay and is limited by the Conti Spur in the north and the Capbreton Canyon in the south (Bourillet *et al.*, 2006). Even though this margin is incised by canyons, the margin is much smoother than the Celtic and Armorican margins (Bourillet *et al.*, 2006). The continental shelf measures only 70 km (Bourillet *et al.*, 2006) and is incised by two main canyons: Cap-Ferret and Capbreton. The head of the latter canyon is the closest to the mainland and has a gentle along-slope profile (Bourillet *et al.*, 2007; Cirac *et al.*, 2001). The canyon flanks of these and the other smaller canyons have a weak slope, no gullies are present and the canyon thalweg is broader than the thalweg of the canyons on the other margins (Bourillet, 2010; De Chambure *et al.*, 2013). The Aquitaine margin has a “tectonic-dominated” instead of a “canyon-dominated” slope (Bourillet *et al.*, 2006) and the different morphology of this margin, compared to the Celtic and Armorican margins, results from two major tectonic phases: (i) crustal distension and rifting, and (ii) partial ocean closing (Bourillet *et al.*, 2006). The Landes drainage system is the only system on the Aquitaine margin and feeds into the Cap-Ferret deep-sea fan via the Cap Ferret, Capbreton and Santander Canyons (Bourillet *et al.*, 2006; Mulder and Zaragosi, 2006). This fan, supplied with sediments originating from the Gironde, the Adour, the Pyrenean and Cantabrian rivers by its drainage system (Brocheray *et al.*, 2014; Schmidt *et al.*, 2014), is less known than the Celtic and Armorican deep-sea fans (Mulder and Zaragosi, 2006). It is known that turbidite deposition began during the Upper Eocene, after a tectonic phase and that the distal Cap-Ferret system and especially the northern levee appeared in the Plio-Pleistocene (Bourillet *et al.*, 2006).

2. Hydrodynamics and sedimentation

There are four different water masses in the Bay of Biscay, which have a different origin and different densities (Durrieu de Madron *et al.*, 1999; Van Aken, 2000a, b). These masses are: (i) the Eastern North Atlantic Water (ENAW), (ii) the Mediterranean Outflow Water (MOW), (iii) the Labrador Sea Water (LSW) and (iv) the Northeast Atlantic Deep Water (NEADW). The ENAW is the shallowest layer and can usually be found between 200 and 600 m water depth. The salinity minimum occurs at 500 m water depth (Durrieu de Madron *et al.*, 1999). This layer primarily originates from the Labrador Current, but may contain an amount of the Antarctic Intermediate Water (AAIW) layer entering the NE Atlantic via the Gulf Stream-North Atlantic Current (Durrieu de Madron *et al.*, 1999; Van Aken, 2000b).

The second layer, the MOW, generally flows between 700 and 1300 m water depth. It is more saline and denser with a salinity maximum at approximately 1000 m depth (Durrieu de Madron *et al.*, 1999; Van Aken, 2000b). This water mass is most remarkable in the south of the Bay of Biscay than in the northern part of this basin (Van Aken, 2000b).

The third layer of the Bay of Biscay is the LSW. It reaches until approximately 2000 m depth (Durrieu de Madron *et al.*, 1999; Van Aken, 2000b). The characteristic salinity minimum of this water mass is less remarkable, because it is mixed with the MOW (Durrieu de Madron *et al.*, 1999; Van Aken, 2000b). Enhanced diapycnal mixing, probably induced by internal tidal waves occurring near the continental slope, causes the two layers to mix (Van Aken, 2000b). However, it is still possible to identify the LSW within the water column with a salinity maximum of 36.88 psu at approximately 1900 m depth (Pingree, 1973, Van Aken, 2000b).

The last layer is the deep NEADW layer. This water mass originates from the LSW, the Iceland Scotland Overflow Water (ISOW), the Lower Deep Water (LDW) and the MOW (Van Aken, 2000a). The salinity maximum occurs between 2000 and 2600 m water depth (Van Aken, 2000a). In the Bay of Biscay, the LSW and the MOW contribute most to this water mass, followed by the ISOW (Van Aken, 2000a).

The hydrodynamic processes taking place in the Bay of Biscay include tidal currents, DSWC (dense shelf-water cascading) and internal waves. These processes modify the temperature, salinity and density of the previously discussed water masses and may play important roles for the sediment and food supply in submarine canyons.

The **general oceanic circulation** is weak and flows anticyclonic in the central regions of the Bay of Biscay (Koutsikopoulos and Le Cann, 1996; Fig. 2) and cyclonic (towards the north) in the northern part of the Bay of Biscay (Mulder *et al.*, 2012). The **shelf current** on the inner shelf flows northwards and is stronger than the outer shelf current that flows southward further from the land; therefore, the residual current is northwards (Koutsikopoulos and Le Cann, 1996; Pingree and Le Cann, 1989; Fig. 2).

Anticyclonic eddies, so called SWODDIES, occur mostly in the southern part of the Bay of Biscay, near the southern Armorican and the Aquitaine margins (Koutsikopoulos and Le Cann, 1996; Pingree and Le Cann, 1992). These currents are generated by the warm surface waters that are moving northwards along the Spanish and French continental shelves (Durrieu de Madron *et al.*, 1999). These eddies may play an important role in the mixing of the ocean waters (Pingree and Le Cann, 1992).

Slope currents are important currents in the Bay of Biscay (Fig. 2). They have a dominant northward or poleward direction, but may vary seasonally with potentially reversed directions (Fig. 2) (Koutsikopoulos and Le Cann, 1996; Pingree and Le Cann, 1989; 1992). It is probably a density-driven and formed by the Mediterranean Outflow Water (Pingree and Le Cann, 1989), one of four water masses in the Bay of Biscay (Durrieu de Madron *et al.*, 1999; Van Aken, 2000a; b). It has a typical speed of 5-6 cm s⁻¹ at 1500 m water depth on the slopes of the Celtic margin (Ivanov *et al.*, 2004; Pingree and Le Cann, 1989; 1990). The slope currents may be related with tidal currents (Pingree and Le Cann, 1990) and is locally affected by the topography of the continental slope (Pingree and Le Cann, 1989; 1990).

Tidal currents also occur in the submarine canyons of the Bay of Biscay, following a semi-diurnal tidal frequency (e.g. Durrieu de Madron *et al.*, 1999; Koutsikopoulos and Le Cann,

1996; Mulder *et al.*, 2012; Pingree and Le Cann, 1989; Fig. 2). These tidal currents are weaker in the southern region of the Bay of Biscay (Aquitaine margin) (Koutsikopoulos and Le Cann, 1996). They can have high speeds, up to 1 m s^{-1} , but are usually lower (Durrieu de Madron *et al.*, 1999; Khripounoff *et al.*, 2014; Mulder *et al.*, 2012). These currents have a down-canyon and up-canyon phase (Mulder *et al.*, 2012), can reach until deep in the canyons (Pichon *et al.*, 2013) and have a high intensity between 400 and 600 m water depth (Gerkema *et al.*, 2004; Lam *et al.*, 2004).

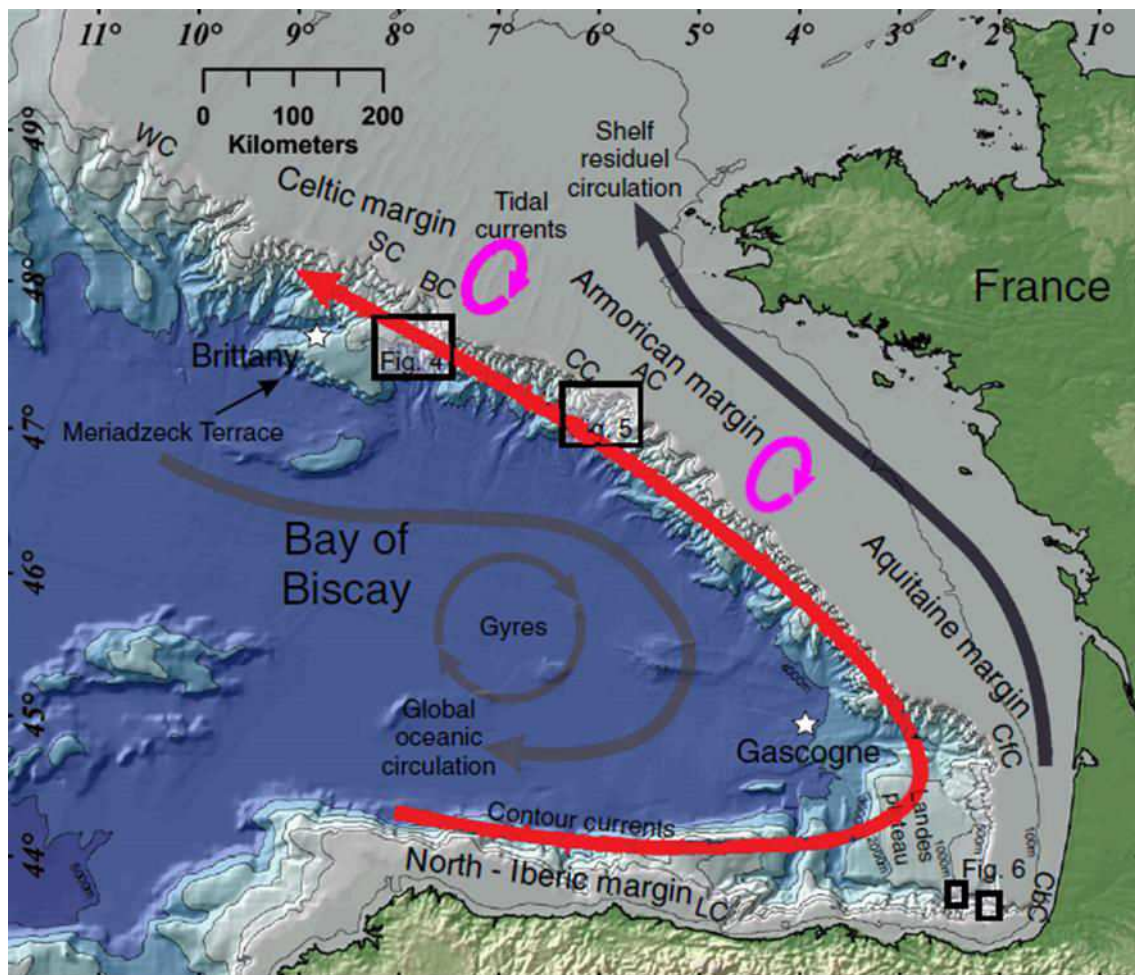


Figure 2: A schematic representation of the hydrological processes at the surface and along the slope in the Bay of Biscay. The global oceanic circulation (in grey) at the surface has a southwards direction. The shelf residual circulation (in black) and the slope current (in red) have dominant northward directions. Other currents in the Bay of Biscay are surface gyres (grey circular arrows) and the tidal currents in the canyons (in pink). WC = Whittard Canyon, SC = Shamrock Canyon, BC = Blackmud Canyon, CC = Crozon Canyon, AC = Audierne Canyon, CFC = Cap-Ferret Canyon, CbC = Capbreton Canyon, LC = Llanes Canyon. Modified from Mulder *et al.* (2012).

Internal waves are also observed in canyons of the Bay of Biscay (Durrieu de Madron *et al.*, 1999; Khripounoff *et al.*, 2014; Mulder *et al.*, 2012; Pichon *et al.*, 2013; Pingree and Mardell, 1985). They can exceed over 50 m at spring tides on the Celtic and Armorican shelf-break, although they do not reach waters deeper than 200 m water depth (Pingree and Mardell, 1985). Internal waves are important in the resuspension of sediment and the creation of intermediate nepheloid layers in Cap Ferret Canyon on the Aquitaine margin (Durrieu de Madron *et al.*, 1999).

DSWC (dense shelf-water cascading) takes place along the continental slope of the Bay of Biscay, due to the rapid change in slope between the flat continental shelf and the steep continental slope. Ivanov *et al.* (2004) identified two sections of typical cascading events on the southern Celtic margin and the adjoining Armorican margin. The DSWC events were mainly caused by the cooling of surface waters and can reach water depths of 500-800 m (Ivanov *et al.*, 2004).

Differences in sedimentation between the margins of the Bay of Biscay exist. As already mentioned in the beginning of this section, the canyons in the southern Bay of Biscay, especially those incising the Aquitaine margin, are smoother compared to the canyons incising the Celtic and (northern) Armorican Margin. The sedimentation rates were also higher in the canyons of the Aquitaine margin (Mulder *et al.*, 2012; Schmidt *et al.*, 2014) that can be linked to lower current speeds in these canyons (Mulder *et al.*, 2012). Due to its close distance to the shore or to the high discharge of rivers connected to the drainage system, this margin received higher amounts of sediment from land (Schmidt *et al.*, 2014). The sedimentation of Cap-Ferret Canyon is complex; the upper canyon (< 500 m water depth) was observed to be a by-pass area where sediment remobilisation takes place as indicated by low sedimentation rates and the higher grain size, the middle canyon between 500 and 1500 m was a deposit centre indicated by the high sedimentation accumulation and the lower canyon (> 1500 m) had similar sedimentation accumulation rates as on the continental shelf near Cap-Ferret Canyon (Schmidt *et al.*, 2014). The sediment deposited in the middle canyon is thought to be flushed to the lower canyon by periodic gravity flows (Schmidt *et al.*, 2014). Similar to Cap-Ferret Canyon, Capbreton Canyon on the same margin had also a high sedimentation accumulation (Mulder *et al.*, 2012). On the contrary, Blackmud and Audierne Canyons on the Armorican margin, were characterised by a low canyon activity, because these canyons were inactive or are active canyons but receive little or no recent sediment or by-passing areas (Mulder *et al.*, 2012).

3. Organic matter

Due to the high sedimentation rates in the canyons of the Aquitaine margin, the canyons incising this part of the Bay of Biscay were also considered as organic deposit centres (Etcheber *et al.*, 1999). Higher average organic carbon concentrations in the first layer of sediment were identified in the upper Cap-Ferret Canyon (500-850 m water depth), the middle canyon (850-2500 m water depth) and the lower canyon (2500-3000 m water depth) than the concentration on the shelf and upper slope (90-500 m water depth) (Etcheber *et al.*, 1999). Nepheloid layers were observed in the same canyon. A layer near the bottom around 2000 m water depth was approximately 500 m thick (Durrieu de Madron *et al.*, 1999). This layer and the intermediate nepheloid layers along the flank extended particularly laterally (Durrieu de Madron *et al.*, 1999).

4. Cold-water corals

4.1. Presence and distribution

The presence of CWCs in the Bay of Biscay was already known since the late 19th century (see Le Danois, 1948). The first attempts to map the distribution of CWCs, including submarine canyons, was done in the early 20th century by Joubin (1922) and Le Danois (1948). Only from the late 2000s, the research to CWCs in submarine canyons increased, aided by the development of stronger bottom trawls and dredges and optical research techniques, e.g. Remotely Operated Vehicles (ROVs). The most investigated canyon in the Bay of Biscay is Whittard Canyon on the Celtic margin (Amaro *et al.*, 2016; Huvenne *et al.*, 2011; Morris *et al.*, 2013; Robert *et al.*, 2015). On the Iberian margin, off Spain, the Avilés Canyon system was investigated for cold-water corals (Altuna, 2013; Altuna and Ríos, 2014; Sánchez *et al.*, 2014). Between Whittard Canyon and the Iberian margin, however, only few studies reported on cold-water corals in a small number of the more than hundred canyons incising the continental margin (De Mol *et al.*, 2011; Joubin, 1922; Le Danois, 1948; Reveillaud *et al.*, 2008).

In the early 1920s, Joubin (1922) reported the presence of the scleractinians *Lophelia pertusa* and *Madrepora oculata* but these species were seen as a nuisance for fishermen. Twenty-five years later, Le Danois (1948) described habitats, or facies, formed by these species, in more detail. In that time, *L. pertusa* and *M. oculata* were called *Lophohelia prolifera* and *Amphihelia oculata*, respectively (Joubin, 1922; Le Danois, 1948). The reef-forming scleractinians *L. pertusa* and *M. oculata*, or “white corals” as they are also called, can either form dense aggregations of colonies (“massifs coralliens”), that emerge from muddy sediments and were rarely over two meters in height along the Atlantic continental slope or they occurred as isolated colonies (Le Danois, 1948). The coral aggregations were observed on Porcupine Bank and Seabight, near Chapelle Bank, Penmarc’h and the “Grande Vasière” on the Armorican margin and on the Galician and Cantabrian margins off Spain at a depth range of 180 to 2000 m (Fig. 3; Le Danois, 1948). Aggregations of another scleractinian, *Dendrophyllia cornigera* or ‘yellow coral’ were observed at ‘Grande Sole’ on the Celtic margin at depths ranging from 200 to 300 m and on Le Danois Bank off Spain at depths ranging from 400 to 500 m (Fig. 3: ‘Massif de corail jaune’). This habitat was observed between 200 and 300 m and between 400 and 500 m respectively.

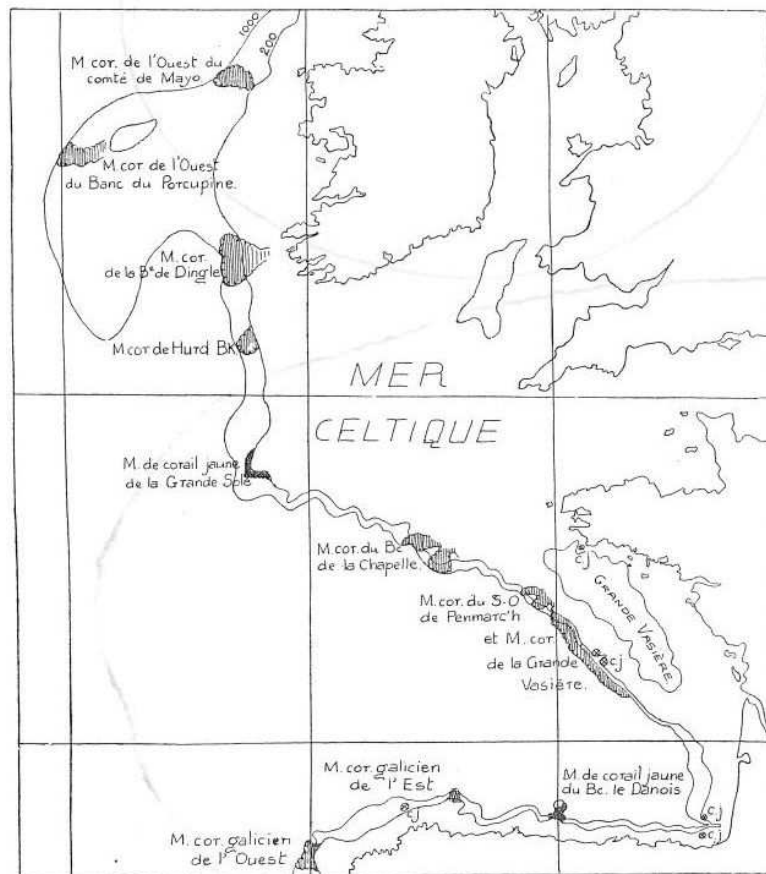


Figure 3: Distribution of *Madrepora oculata* and *Lophelia pertusa* habitats ('M. cor') as well as the habitat constructed by the 'yellow coral' *Dendrophyllia cornigera* ('M. de corail jaune') along the Irish, French and Spanish continental margin. Reproduced from Le Danois (1948).

Besides these three colonial scleractinians, solitary scleractinians were also observed in this basin. A total of 85 species were included in a large geographical study to solitary and colonial scleractinians by Zibrowius (1980). He examined specimens collected in the North-East Atlantic between the north of Norway until Senegal, around Iceland, the Azores and Cape-Verde Island and in the Mediterranean Sea from all depth ranges. From the 80 species in the Atlantic Ocean, only 5 species have been described for the continental shelf of the northern Bay of Biscay, of which the solitary *Caryophyllia smithii* was the most abundant. On the continental slope, more scleractinian species occur, including *L. pertusa*, *M. oculata* and *D. cornigera*, but Zibrowius (1980) did not specify these species any further. Between 45° and 43° N latitude, southern Bay of Biscay, 34 species were collected.

Reveillaud *et al.* (2008) compiled and mapped all historical scleractinian records (Fig. 4), including occurrences reported by the previously described work from Joubin (1922), Le Danois (1948) and Zibrowius (1980). New records of grab samples taken during two cruises in 1997 and 2004 have been added to the database. A total of 34 scleractinian species were recorded in depth ranges between 10 and 5000 m water depth. This gives the best representation of scleractinians in the Bay of Biscay, but concerns species occurrences and only scleractinians are included. Further, it includes data that has a poor georeferenced location, mainly data from before the GPS-era.

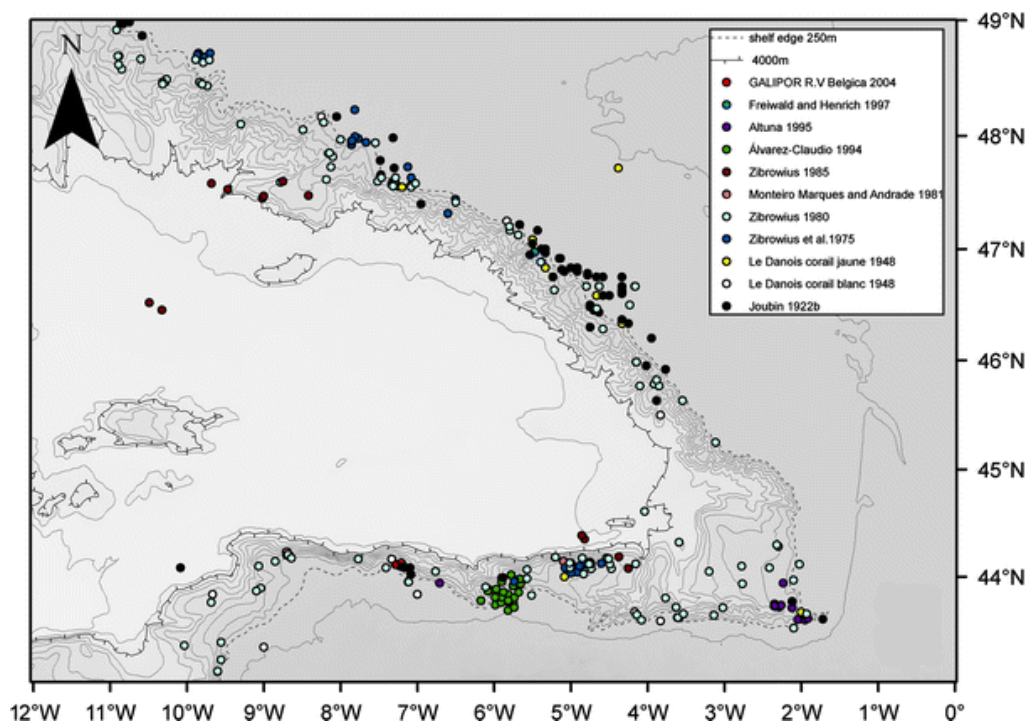


Figure 4: A map with occurrences of scleractinians in the Bay of Biscay. Reproduced from Reveillaud *et al.* (2008).

Within a few canyons of the Bay of Biscay, detailed information is available, because it involves recent data collected by an ROV, that usually has a good positioning system. Further, these studies give an *in situ* view of the CWC habitats and their communities (see section 4.2.). Most of these studies described habitats composed by *L. pertusa* and *M. oculata*. De Mol *et al.* (2011) established eleven facies of which eight consisted of scleractinian framework, live colonies or debris in Penmarc'h and Guilvinec Canyons. These scleractinian facies differed in densities, ranging from patchy corals to dense coral fields including live colonies of *M. oculata* and *L. pertusa*. The dense coral fields coincided mostly with a very rough seafloor and big boulders up to 1 m in height (De Mol *et al.*, 2011).

The most abundant coral species in Whittard Canyon are *L. pertusa*, the gorgonians *Primnoa* sp., *Acanthogorgia* sp. and *Acanella* sp. and the soft coral *Anthomastus* sp. occurring between 880 to 3300 m water depth (Huvenne *et al.*, 2011; Morris *et al.*, 2013; Robert *et al.*, 2015). Most corals in this canyon colonized steep areas, such as large boulders or vertical cliffs. A new type of coral habitat was a 1600 m long vertical cliff including overhangs of which ~70% was covered by dense colonies of *L. pertusa* at a water depth of approximately 1650 m (Huvenne *et al.*, 2011). Another cliff habitat in another branch of Whittard Canyon was dominated by gorgonians, e.g. *Primnoa* sp., mixed with *L. pertusa* (Huvenne *et al.*, 2011; Morris *et al.*, 2013). Colonies of *M. oculata* and *Solenosmilia variabilis* were also observed as well as large aggregations of *Kophobelemnion* sp. and *Pennatula aculeata* between 800 and 1000 m depth (Robert *et al.*, 2015). In Dangeard and Explorer Canyons (South West Approaches), two canyons south of Whittard Canyon that share the same channel, *L. pertusa* colonies and rubble were observed (Davies *et al.*, 2014; Howell *et al.*, 2010). The authors of these two studies also observed caryophyllids and *Kophobelemnion stelliferum* on mixed substrate and on muddy

bottoms, respectively (Davies *et al.*, 2014; Howell *et al.*, 2010). Sea pen aggregations on muddy bottoms between 500 and 1000 m water depth were already observed by Le Danois (1948). These aggregations showed differences in composition between the north, near Ireland, (*K. stelliferum*, mixed with *Umbellula* spp.) and the south of the NE Atlantic margin (*Pennatula* spp.) (Fig. 5).

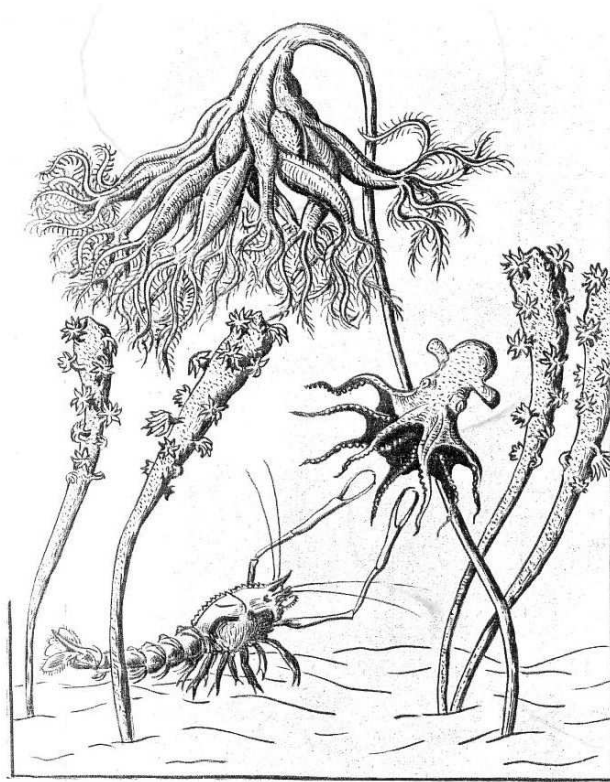


Figure 5: A drawing of sea pens on mud. The community is composed by the sea pen *Kophobelemnion stelliferum* (four colonies), the sea pen *Umbellula* spp. (top), an octopus *Grimpoteuthis umbellata* and the crustacean *Polycheles typhlops*. Reproduced from Le Danois (1948)

In the Spanish part of the Bay of Biscay, La Gavierra Canyon in the Avilés Canyon system, Sánchez *et al.* (2014) observed also scleractinian facies with an ROV. The facies included coral reef, coral fields, dead coral framework, isolated coral reef formations, hard substrate with patchy corals, rippled sediments and patchy corals and rippled sediments and dead coral. CWC facies were constructed by *L. pertusa*, *M. oculata* and *S. variabilis*. Other studies in the same canyon system also observed *L. pertusa* and *M. oculata* (Altuna, 2013; Altuna and Ríos, 2014), *Caryophyllia calveri*, *Desmophyllum cristagalli* (Altuna, 2013), *S. variabilis*, *Enallopsammia rostrata* and *D. cornigera* (Altuna and Ríos, 2014).

Variations in coral species present on Irish, French and Spanish margins existed, e.g. the gorgonian species between the Irish and Bay of Biscay margins differed, where one species was replaced by another species of the same genus, e.g. *Ceratoisis grayi* (accepted name *Keratoisis grayi*) and *Callogorgia flabellum* replaced by the more southern occurring *Ceratoisis flexibilis* (accepted name *Keratoisis flexibilis*) and *Callogorgia verticillata*, respectively (Le Danois, 1948).

A latitudinal gradient is suggested for these two species in the NE Atlantic, with *L. pertusa* being more abundant in the north and *M. oculata* being more dominant in the south (Arnaud-Haond *et al.*, 2015). This is consistent with observations of *L. pertusa* as dominant species off

Norway (e.g. Mortensen *et al.*, 2001) and *M. oculata* as dominant species in the Mediterranean Sea (e.g. Fabri *et al.*, 2014; Gori *et al.*, 2013; Orejas *et al.*, 2009). In the Bay of Biscay, *M. oculata* and *L. pertusa* systematically co-occurred (Arnaud-Haond *et al.*, 2015), with a slight dominance of *M. oculata* (Arnaud-Haond *et al.*, 2015; De Mol *et al.*, 2011).

The distribution of reef-building scleractinians in the Bay of Biscay is controlled by ice age cycles and its oscillations. The Bay of Biscay supported a continuous presence of *L. pertusa* and *M. oculata* over the past 4.5 kyr and may go back to even more than 7 kyr, as indicated by age determinations (De Mol *et al.*, 2011; Frank *et al.*, 2011), but the development of the CWC reefs varied over time (Frank *et al.*, 2011). In more recent times, the early to mid-Holocene, the number of younger corals summed per 2500 years age-classes was higher than the number of older corals which was expected considering the climate change during this period (Frank *et al.*, 2011).

4.2. *Faunal communities*

Most of the communities investigated so far were associated to *L. pertusa* and/or *M. oculata*. Communities have been defined according to dominant species, substrata and depth from trawl data (Le Danois, 1948) or image analysis (De Mol *et al.*, 2011; Huvenne *et al.*, 2010; Sánchez *et al.*, 2014). Howell *et al.* (2010) and Davies *et al.* (2014) used statistical means to establish megafaunal assemblages on image footage from a drop-frame camera in Dangeard and Explorer Canyons (South West Approaches). Most of the investigated communities were associated to *L. pertusa* and/or *M. oculata*.

Le Danois (1948) reported that *L. pertusa*/*M. oculata* communities included the solitary coral *D. dianthus*, hydroids, gorgonians, the mushroom coral *Anthomastus* sp., sponges, bryozoans, annelids (including the symbiont of reef-building scleractinians *Eunice floridana*, what is probably *Eunice norvegica*, a known symbiont for *L. pertusa* and *M. oculata*), barnacles, ophiuroids, crinoids, bivalves, crustaceans and fish (Fig. 6; Le Danois, 1948).

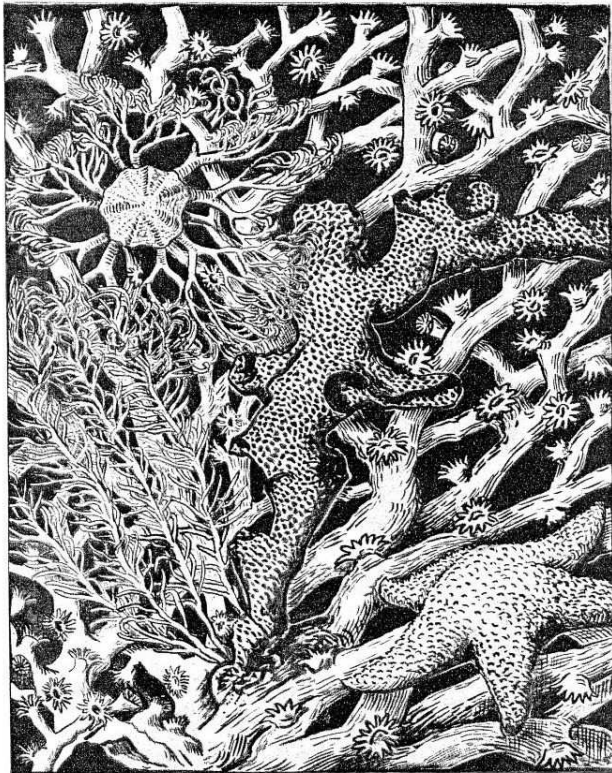


Figure 6: A drawing of the scleractinian community. Branches of *Madrepora oculata* with its associated species: the hexactinellid sponge *Aphrocallistes beatrix* (centre), the gorgonian *Callogorgia flabellum* (left), the ophiuroids *Gorgonocephalus caputmedusae* (top left) and the asteroid *Poraniamorpha hispida* (bottom right). Reproduced from Le Danois (1948).

The recent studies have significantly expanded the list of species associated with *L. pertusa* and *M. oculata* in the Bay of Biscay. Multiple authors reported on the encrusting sponge *Hexadella* spp. and a variety of other sponges, *Neopycnodonte zibrowii* oysters, *Acesta* bivalves and other molluscs, *Caryophylla* sp., cerianthids, zoanthids, actinians, incl. Halcampoidid anemones, hydroids, crinoids, incl. *Koehlermetra porrecta*, asteroids, including brisingids, ophiuroids, echinoids, e.g. *Cidaris cidaris* and *Echinus* sp., annelids, e.g. serpulids, brachiopods, bryozoans, ascidians, several arthropods, incl. the squatlobster *Munida* sp. and *Pandalus borealis* shrimp, and fish species (Davies *et al.*, 2014; De Mol *et al.*, 2011; Howell *et al.*, 2010; Huvenne *et al.*, 2011; Sánchez *et al.*, 2014). Illustrations of different scleractinian facies given by De Mol *et al.*, (2011) showed various species of gorgonians (e.g. *Narella versluysi*), antipatharians (*Trissopathes* spp., *Leiopathes* spp., *Parantipathes* spp.), sponges (e.g. *Geodia* spp.), crinoids, echinoids, the squatlobster *Munida* sp., actinians and solitary scleractinians. The diversity of the communities associating with *L. pertusa*/*M. oculata* habitat is generally higher than the diversity associated with other (CWC) habitats, e.g. soft bottom habitats composed by *A. arbuscula* and/or *K. stelliferum* and hard substrate habitats composed by the soft coral *Anthomastus* sp. as observed in Whittard Canyon and the South West Approaches (Davies *et al.*, 2014; Robert *et al.*, 2015).

The area above the scleractinian habitat, ‘facies supracorallien’, was characterised by brachiopods, while the area below the scleractinian habitats (‘facies infracorallien’), usually composed by mud and rubble, was characterised by a variety of animals including the glass sponges *Pheronema carpenteri*, *Asconema setubalense*, *Mellonympha velata* and *Regadrella phoenix*, the demosponges *Asbestopluma pennatula* and *Cladorhiza abyssicola* as well as the echinoid *Conocrinus lofotensis*.

Several taxa were seen to associate with *K. stelliferum* habitats and included cerianthids, ophiuroids, incl. *Ophiactis balli*, crinoids, incl. *Pentametrocrinus atlanticus*, a Halcampoididae actinian, and the bamboo coral *Acanella* sp. (Davies *et al.*, 2014; Howell *et al.*, 2010).

4.3. Environmental conditions and response to climate change

The distribution of CWCs is primarily determined by the substrate type, the topography and the hydrology. Most CWCs need hard substrate, although sea pens and some species of gorgonians and antipatharians are dependent on soft sediment (Roberts *et al.*, 2009; Wagner *et al.*, 2012; Williams, 2011). In addition, the slope is also an important factor for CWCs. *L. pertusa* and *S. variabilis* have been observed on vertical features, e.g. cliffs, and overhangs, especially in Whittard Canyon (Huvenne *et al.*, 2011) or on steep areas in Penmarc'h and Guilvinec Canyons (De Mol *et al.*, 2011). CWC habitat can exist on this steep topography due to canyon processes, such as internal tides, and organic carbon transport as well as the minimal impact of human activities as suggested by Huvenne *et al.* (2011). In addition, the colonies could not be smothered by sediment because of their position against the vertical wall or under overhangs (Huvenne *et al.*, 2011). Models predicting abundance, density and diversity of megafauna in Whittard Canyon suggested that slope indeed influenced the abundance, densities and diversity of the megafauna, as well as finer-scale variations in sea-bed morphology and depth (Robert *et al.*, 2015). Rugosity, geomorphology and Bathymetric Position Index (BPI) were important factors influencing the habitat suitability models of coral reefs in La Gaviera Canyon (Sánchez *et al.*, 2014), suggesting that the topography of the seafloor is important for the distribution of especially *L. pertusa* in this canyon.

Water density is also an important factor for CWCs. Dullo *et al.* (2008) has observed that CWCs had a particular density envelop, that corresponded to the MOW (Mediterranean Outflow Water), even though Porcupine Seabight, off Ireland, was the most southern location included in this study. However, deep-water scleractinian communities in Whittard, Penmarc'h, Guilvinec and La Gaviera Canyons were observed in a similar density envelope, also corresponding to the MOW (De Mol *et al.*, 2011; Huvenne *et al.*, 2011; Sánchez *et al.*, 2014). Huvenne *et al.* (2011), however, observed live scleractinians below the border between the MOW and the deeper North-Atlantic Deep Water (NADW) layer. The authors suggested that scleractinians could occur in this deep layer, because the specific hydrodynamic regimes, e.g. tidal currents and DSWC, could bring both larvae and food through this density boundary to deeper areas in submarine canyons. The nepheloid layers that are observed at these water depths (between 1200 and 2000 m) have high levels of particulate organic carbon that is between the optimum range of CWCs (Huvenne *et al.*, 2011) and thus suggest that food was available below the MOW-NADW boundary.

In Penmarc'h and Guilvinec Canyons, coral rubble was shallower (250-350 m water depth) and older (7.4-9.7 kyr) than live scleractinian colonies (350-950 m; 1.2-2.3 kyr) (De Mol *et al.*, 2011). These depth and age distribution patterns suggest a migration of scleractinians along the continental slope that could be explained by the rising of the sea level and the warming of surface waters since the last maximum glacial period of 11.5 kyr ago (De Mol *et al.*, 2011).

Global warming, changing the water temperature and ocean circulation, may have an effect on the dispersal and the connectivity of organisms (Lett *et al.*, 2010). Dispersion models for coastal invertebrates showed that an increase of temperature has consequences as earlier spawning events and a shorter planktonic larval period (Ayata *et al.*, 2010).

Water circulation and density could also be affected by water temperature alternations and may have consequences for the important slope current of the Bay of Biscay (Pingree and Garcia-Soto, 2014) and, thus, for the production of internal waves and exposition of hard substrate (Allen and Durrieu de Madron, 2009; Pingree and Gracia-Soto, 2014; Van Rooij *et al.*, 2010). In addition, it may have multiple changes on the seasonality of planktonic blooms as well as on the quantity and quality of the primary production that may determine the reproduction periods and the physical state of cold-water corals (Brooke and Järnegen, 2013; Chust *et al.*, 2014; Harrison, 2011; Pingree and Garcia-Soto, 2014).

Ocean warming forces cold-water corals to move to deeper waters or to higher latitudes, where the water is usually colder. However, the shallowing of the calcite/aragonite saturation horizons, chemical compounds indispensable for CWCs, prevents CWCs to move to deeper areas with consequences as the extinction of certain CWCs species or a northward shift of CWC communities. A good example would be the reef-building scleractinians *L. pertusa* and *M. oculata*. The former species is dominant in the colder regions at higher latitudes (e.g. Arnaud-Haond *et al.*, 2015; Mortensen *et al.*, 2001), whereas the latter species wins in abundances in warmer waters, including the Bay of Biscay (Arnaud-Haond *et al.*, 2015; De Mol *et al.*, 2011) and the Mediterranean Sea (Fabri *et al.*, 2014; Gori *et al.*, 2013; Orejas *et al.*, 2009). It could be expected that the geographical range of the high-temperature tolerant *M. oculata* will increase to the north, whereas the distribution of *L. pertusa* will decrease, because it will reach its most northern limit. Age determinations of *L. pertusa* and *M. oculata* suggested that the temperate North-East Atlantic always sustained and will sustain CWC growth, including warm climate periods (Frank *et al.*, 2011). The authors also mentioned, however, that the expected warming of the oceans, combined with the reduction of Arctic sea ice sheet will promote a northward movement of reef-building scleractinians in the Arctic Ocean, but that this northwards colonisation may be prevented by the rapidity of the temperature changes, coupled with ocean acidification, changes in circulation and food supply, and the occurrence of deep-sea trawling (Frank *et al.*, 2011).

Fisheries, especially bottom trawling, could also have an effect on CWCs. It could contribute to the explanation of the distribution patterns of live reefs and rubble observed by De Mol *et al.* (2011); the authors observed coral rubble in shallower settings characterised by a smooth topography and live reefs in deeper settings characterised by a steep topography. The smoother interflues and upper slope are easier accessible to bottom trawls with a lower risk to damage fishing gear. Especially the upper slope, but also parts of the interflues, are relatively shallow compared to the canyon flanks. In addition, trawling could bring scleractinian colonies fished in one place to another place where pieces of live coral could fall and settle. This may also be an explanation of the younger *L. pertusa* colony (1.4 ka) within the shallow-water older CWC settings in Penmarc'h and Guilvinec Canyons (De Mol *et al.*, 2011). Submarine canyons are not completely free from impact of human activities as reviewed by Fernandez-Arcaya *et al.*

(2017). Observations in Whittard canyon – a trawl mark was seen on the seabed and a lost longline entangled in *L. pertusa* colonies – illustrate the fisheries impact (Huvenne *et al.*, 2011).

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Chapter 3

Cold-water coral habitats in submarine canyons of the Bay of Biscay

Résumé français

Habitats coralliens dans les canyons sous-marins du Golfe de Gascogne

1. Introduction

Les canyons sous-marins sont des structures géologiques complexes qui incisent un grand nombre de plateaux continentaux de l'océan mondial (Harris et Whiteway, 2011). Les canyons constituent un environnement idéal pour le développement des coraux d'eau froide, en raison de leur topographie complexe, des processus hydrodynamiques et de la grande hétérogénéité du substrat (De Leo *et al.*, 2010 ; Mortensen et Buhl-Mortensen, 2005 ; Orejas *et al.*, 2009 ; White *et al.*, 2005).

Les coraux d'eau froide ou coraux d'eau profonde peuvent construire des habitats, tels que les récifs constitués par les espèces *Lophelia pertusa* et *Madrepora oculata* (Roberts *et al.*, 2006) et des jardins de coraux formés par des antipathaires, gorgones ou pennatules (Freiwald *et al.*, 2004). Ces habitats pourraient fournir des refuges et fonctionner comme des zones d'alimentation, des frayères ou des nurseries pour de nombreuses espèces (Roberts *et al.*, 2006, Freiwald *et al.*, 2004). Les récifs sont également supposés être caractérisés par une forte biodiversité (Freiwald *et al.*, 2004 ; Roberts *et al.*, 2009).

Les coraux d'eau froide ont un faible taux de croissance et une longévité élevée (par. ex. Freiwald *et al.*, 2004 ; Roberts *et al.*, 2009). De ce fait, et parce qu'ils sont situés dans des zones le plus souvent accessibles, ils sont particulièrement sensibles aux activités humaines, comme la pêche et l'industrie pétrolière (Ramirez-Llodra *et al.*, 2011 ; Roberts *et al.*, 2006). Ainsi, les coraux d'eau froide font partie des habitats marins sensibles pour plusieurs initiatives internationales de préservation (OSPAR, ICES, Habitats Directives). Les canyons sous-marins sont considérés comme des refuges naturels pour certains habitats coralliens (Fernandez-Arcaya *et al.*, 2017 ; Huvenne *et al.*, 2011).

Les cartes de distribution d'habitats sont un outil privilégié pour bâtir une stratégie de préservation. Les systèmes de classification aident à la création des cartes d'habitats détaillées et intégratives. Ils permettent l'utilisation d'une terminologie standardisée sur une grande région. Un système de classification des biotopes (ou habitats) coralliens a été développé pendant le projet européen CoralFISH du FP7 (Davies *et al.*, 2017).

La marge continentale du Golfe de Gascogne, étudiée ici, est incisée par une centaine de canyons sous-marins (Bourillet *et al.*, 2006). Bien que la présence de scléractiniaires et des récifs soient connues depuis le début du vingtième siècle (Joubin, 1922 ; Le Danois, 1948), il n'y a eu que très peu d'études sur les coraux d'eau froide dans le Golfe de Gascogne français depuis (De Mol *et al.*, 2011 ; Reveillaud *et al.*, 2008 ; Zibrowius, 1980). La majorité de ce bassin reste toujours inexplorée.

Dans cette étude, nous rendons compte des investigations sur la présence des coraux d'eau froide dans les canyons sous-marins du Golfe de Gascogne, en basant sur des explorations par

un ROV (*Remotely Operated Vehicle*) et une caméra tractée. Nous avons utilisé le système de classification des habitats coralliens pour définir ceux que nous avons observés sur les images rapportées par ces deux engins sous-marins. Les objectifs de cette étude étaient : (i) identifier les habitats coralliens dans les canyons sous-marins du Golfe de Gascogne, (ii) identifier les espèces coralliennes et leur abondance, leur densité ainsi que la composition et la diversité de ces habitats, (iii) étudier la distribution des habitats coralliens du Golfe de Gascogne, et (iv) explorer l'influence des facteurs environnementaux (température, salinité, densité de l'eau, profondeur, dérivées de la bathymétrie et géomorphologie) sur la présence et la distribution des habitats coralliens.

2. Matériels et méthodes

La pente continentale du Golfe de Gascogne est incisée par une centaine de canyons sous-marins et comprend trois marges (Fig. 1) : (i) la marge Celtique, (ii) la marge Armoricaïne, et (iii) la marge Aquitaine. Les marges Celtique et Armoricaïne sont caractérisées par des éperons et canyons (Bourillet *et al.*, 2006). Les canyons qui incisent la marge Celtique et le nord de la marge Armoricaïne présentent des éléments géomorphologiques communs en particulier au niveau de la tête du canyon, comme les falaises (Bourillet *et al.*, 2010). La marge Armoricaïne centrale comprend une alternance de canyons larges ou étroits (Bourillet *et al.*, 2010). Les canyons qui incisent la marge Armoricaïne méridionale sont beaucoup plus lisses que les canyons au nord et ils ont des flancs plus réguliers et sédimentaires (Bourillet *et al.*, 2010). Enfin, les canyons de la marge Aquitaine ont une pente faible et ils n'ont pas de marge ou falaise (Bourillet, 2010 ; De Chambure *et al.*, 2013).

Plusieurs processus hydrodynamiques sont à l'œuvre dans le Golfe de Gascogne qui influencent la production primaire et le transport de la nourriture dans les canyons sous-marins, par exemple les courants de marée, les vagues internes et un courant de pente qui a une direction dominante vers le Nord (Koutsikopoulos et Le Cann, 1996 ; Mulder *et al.*, 2012 ; Pingree et Le Cann, 1989 ; 1992).

Les données de cette étude ont été acquises dans 24 canyons et 3 sites sur des interfluves ou du haut de pente contigu entre deux canyons. Quarante-six plongées ont été réalisées pendant sept campagnes entre 2009 et 2012 (BobGeo, BobGeo 2, BobEco, Evhoe 2009, 2010, 2011 et 2012). Des images ont été acquises par les caméras verticales du ROV Victor 6000 pendant 13 plongées de la campagne BobEco et du système de caméra tracté SCAMPI pendant 33 plongées réalisées au cours des 5 autres campagnes. Des images ont été extraites des vidéos du ROV pour permettre la comparaison avec les photos prises par le système tracté.

Chaque image répondant aux critères du contrôle qualité (altitude, netteté, visibilité) a été analysée. Les habitats sont définis selon le système de classification de CoralFISH incluant une caractérisation des espèces coralliennes formant l'habitat, et du substrat (Davies *et al.*, 2017). Un biotope (ou habitat) est considéré comme une aire minimale de l'ordre 25 m² où l'épifaune remarquable, en incluant les coraux d'eau froide, est observée de manière répétitive et continue.

Les zones couvertes par les plongées sont donc découpées en segments d'habitats. Un segment d'habitat est défini comme toutes les images contigües qui montrent le même habitat, jusqu'à ce qu'un autre habitat soit observé sur une image.

Un sous-ensemble des images est créé par sélection des images sur un pas temps d'une minute depuis le début de la plongée. Sur ce sous-ensemble des images ont été annotés :

- Les taux de couverture en substrat dur, meuble ou biogénique. Le substrat biogénique incluant les scléactiniaires récifaux *L. pertusa*, *M. oculata* et *Solenosmilia variabilis*.
- Les espèces coralliennes, identifiées au niveau de résolution taxinomique le plus fin possible et dénombrées.

A l'aide du SIG, à chaque segment d'habitat a été attribué des valeurs moyennes de variables géologiques, déduites de la bathymétrie telles que la profondeur, la pente et la rugosité et de variables hydrologiques, comme la température, la salinité et la densité de l'eau. Les variables géologiques ont une résolution de 100 m et les variables hydrologiques ont une résolution de 0.083° latitude (~10 km) à l'échelle du Golfe de Gascogne.

Deux classifications géomorphologiques ont par ailleurs été produites à partir d'une interprétation semi-automatique des données de bathymétrie et ses dérivés, à une résolution de 100 m à l'échelle du Golfe de Gascogne et à une résolution de 15/25 m pour quatre zones sur la marge Armoricaire nord, central et du sud ainsi que la marge Aquitaine (De Chambure *et al.*, 2013). Chaque image annotée a été associée une classe géomorphologique.

3. Résultats

Onze types d'habitats coralliens ont été observés dans les canyons sous-marins du Golfe de Gascogne, présents sur 4191 images (sur un total de 14.874 images analysées) (Fig. 2). Ces habitats sont des récifs de coraux, débris de coraux, scléactiniaires coloniaux sur substrat dur, scléactiniaires solitaires sur substrat dur, antipathaires/gorgones sur substrat dur, assemblage mixte de coraux sur substrat dur, scléactiniaires coloniaux sur substrat meuble, scléactiniaires solitaires sur substrat meuble, gorgones sur substrat meuble, pennatules sur substrat meuble et coraux mixtes sur substrat meuble. L'habitat de coraux solitaires sur substrat dur étant marginal ; il a été exclu des analyses ultérieures.

Soixante-deux morphotypes coralliens ont été observés dans dix habitats coralliens : 6287 individus de 59 morphotypes ou espèces non récifales et les trois scléactiniaires récifaux *L. pertusa*, *M. oculata* et *S. variabilis*.

Les densités de coraux étaient plus élevées dans les habitats biogéniques (récifs et débris de coraux) et les habitats coralliens sur substrat dur que dans les habitats coralliens sur substrat meuble (Table 3). De la même façon, **la diversité de coraux** dans les habitats coralliens sur substrat meuble, formés par des scléactiniaires solitaires, gorgones, pennatules ou coraux mixtes, était inférieure à celle des habitats coralliens sur substrat dur et des habitats biogéniques (Fig. 3 ; Table 3).

Les habitats coralliens sur substrat dur et les habitats biogéniques partageaient des **compositions similaires d'espèces** (Fig. 4A). Néanmoins, les scléactiniaires récifaux dominants étaient différents entre les habitats coralliens sur substrat dur et les habitats biogéniques : *L. pertusa* et *M. oculata* dominent les habitats biogéniques et *S. variabilis* domine l'habitat des scléactiniaires coloniaux sur substrat dur (Fig. 4B). Les habitats sur substrat meuble étaient **quasi mono-spécifiques** (Fig. 4A) et dominés par la gorgone *Acanella arbuscula*, les pennatules *Kophobelemnion stelliferum* ou *Distichoptilum gracile*, ou les scléactiniaires solitaires Flabellidae sp. 1 et Caryophyllidae sp. 7.

Les habitats coralliens ont été observés dans l'ensemble des 24 canyons et sur deux des trois sites explorés sur des interfluves ou haut de pente contigu entre deux canyons adjacents. Les **patrons de distribution des habitats coralliens à l'échelle régionale** sont (Fig. 6) : les habitats coralliens sur substrat meuble dominent la marge Aquitaine et les habitats scléactiniaires vivants sont absents sur cette marge et le sud de la marge Armoricaire. **A l'échelle du canyon**, les scléactiniaires ont été observés plus fréquemment sur les flancs orientés au nord-ouest et les pennatules sur les flancs sud-est (Fig. 9B).

Les habitats coralliens ont surtout été observés **entre 600 et 1200 m de profondeur** (Fig. 8) ; ce sont des débris de coraux qui ont été observés à la moindre profondeur et des antipathaires/gorgones sur substrat dur dans les zones plus profondes. La distribution des habitats coralliens n'est expliquée qu'à 9.1% par les conditions environnementales incluant la profondeur, la température, la salinité et la densité de l'eau.

Nous avons cependant observé une influence de la géomorphologie : (i) les habitats coralliens vivants ont été observés plus fréquemment dans les canyons que sur les interfluves ou en haut de pente contigu au plateau, tandis que les débris de coraux ont été observés plus fréquents sur les interfluves et les hauts de pente contigus au plateau (Fig. 9A), et (ii) la pente influence la distribution des habitats coralliens de la manière significative (Fig. 9B) ; cette influence était plus forte sur les habitats coralliens sur substrat dur et les habitats biogéniques que les habitats coralliens sur substrat meuble. La distribution de débris de coraux est favorisée par des pentes plus faibles que celle des autres habitats.

4. Discussion

Les patrons de distribution des habitats coralliens à l'échelle du Golfe de Gascogne – une dominance d'habitats coralliens sur substrat meuble dans les canyons sous-marins sur la marge Aquitaine et une absence des habitats scléactiniaires vivants dans le sud du Golfe de Gascogne alors qu'ils colonisent les canyons du Nord et central du Golfe semblent être liés à l'hétérogénéité de substrat : les canyons du sud du Golfe de Gascogne sont plus lisses et sédimentaires du fait d'une morphologie et d'une hydrologie différente de celle des canyons plus au nord du Golfe de Gascogne. A l'échelle d'un canyon, la distribution des habitats coralliens varie également, dû à une asymétrie d'hydrodynamique dans les canyons. Cette asymétrie a causé l'érosion des flancs du nord-ouest en favorisant la colonisation de

scléactiniaires qui préfèrent le substrat dur et la sédimentation des flancs du sud-est en favorisant les habitats coralliens sur substrat meuble, par exemple les pennatules.

Les habitats biogéniques et les habitats coralliens sur substrat dur partagent des morphotypes coralliens, si l'on exclue les trois scléactiniaires récifaux. Malgré la dominance du substrat meuble dans l'habitat scléactiniaires coloniaux sur substrat meuble, l'assemblage corallien de cet habitat est similaire aux compositions des habitats biogéniques ; les espèces coralliennes qui préfèrent le substrat dur, pourraient s'installer sur la structure scléactiniaire émergente de substrat meuble. Les assemblages coralliens sur des habitats sur substrat meuble diffèrent les uns des autres, montrant un *turnover* d'espèces plus élevé que celui des substrats durs.

Les habitats coralliens du Golfe de Gascogne partagent des conditions environnementales similaires (hydrologie, profondeur, dérivées de bathymétrie), du moins aux résolutions auxquelles ces facteurs environnementaux étaient disponibles pour cette étude. Il y a une en effet une grande différence entre la résolution des habitats, dont la majorité mesure moins de 100 m de long, et la résolution des facteurs environnementaux qui ont une résolution entre 100 m et 0.083° latitude (~ 10 km). Cette grande différence pourrait expliquer que nous n'avons pas trouvé un environnement spécifique pour les habitats coralliens. Ces résultats montrent la nécessité d'un jeu de données d'une meilleure résolution des facteurs environnementaux pour permettre de préciser les relations entre environnement et habitats coralliens et donc de prédire leur distribution. De telles cartes de la distribution observée et prédites des différents habitats sont en effet nécessaires pour la préservation de ces écosystèmes vulnérables. Les systèmes de classification d'habitat donnent l'information sur la distribution des habitats plus rapidement qu'une analyse détaillée à l'échelle des espèces et sont donc également une aide pour les politiques de gestion. Cependant, les systèmes de classification d'habitat peuvent également limiter la compréhension de la biologie et l'écologie des espèces.

Les résultats de cette étude soutiennent l'hypothèse que les canyons sous-marins pourraient fonctionner comme des **refuges pour les habitats coralliens** (Fernandez-Arcaya *et al.*, 2017 ; Huvenne *et al.*, 2011) : les habitats scléactiniaires vivants ont été observés plus fréquemment dans les canyons et sur une pente plus forte que les débris de coraux qui ont été observés sur l'interfluve et les hauts de pente contigus au plateau et sur des zones plus plates. Les zones moins profondes et moins accidentées, sont *a priori* plus faciles à chaluter. Même si la pêche au chalut pourrait expliquer ces résultats, les causes naturelles liées à des changements environnementaux ne peuvent pas être exclues.

Les mesures de protection sont rares dans le Golfe de Gascogne et ne concernent pas les habitats benthiques. Cette étude a déjà alimenté une proposition pour définir des grands secteurs pour un réseau de sites de Natura 2000 pour la protection des habitats récifaux sous la Directive Habitats Faune Flore (MNHN-SPN et GIS-Posidonie, 2014). Le processus de la désignation d'un réseau de Natura 2000 incluant des canyons sous-marins sera un pas en avant pour la préservation des habitats profonds dans l'Atlantique français. Ce réseau cependant n'inclura pas les habitats coralliens sur substrat meuble, puisque ces habitats ne répondent pas à la définition de récif donnée par la directive. Les gorgones, pennatules et scléactiniaires solitaires

qui dominent ces habitats sont reconnus comme des espèces vulnérables. La distribution de ces habitats localisés sur les fonds meubles des interfluves et des canyons coïncident également probablement avec des zones propices au chalutage. Il est donc nécessaire de mieux comprendre leur distribution et leur sensibilité afin d'évaluer leur besoin de préservation.

5. Conclusion

Cette étude inclut 24 canyons et les résultats qui sont rapportés ici augmentent donc largement la connaissance de la distribution des habitats coralliens dans les canyons sous-marins du Golfe de Gascogne. A l'échelle régionale, le sud du golfe de Gascogne se caractérise par une dominance des habitats coralliens sur substrat meuble et une absence des habitats à scléactiniaires vivant. La nature du substrat est un facteur déterminant de la distribution et la composition des habitats à l'échelle régionale comme à l'échelle d'un canyon. En termes de composition, deux types d'assemblages de coraux se distinguent, ceux des habitats de substrat dur ou biogénique et ceux de substrat meuble. Les habitats coralliens sur substrat meuble se caractérisent par une diversité intra-habitat réduite mais un *turnover* d'espèces inter-habitat élevé. Le chevauchement des conditions environnementales associées aux différents habitats coralliens pourrait être lié à la faible résolution spatiale des données environnementales. Les données manquent également sur des facteurs potentiellement clés dans la distribution des coraux tels que les vitesses ou l'exposition aux courants. Les classes géomorphologiques semblent fournir une indication sur l'environnement favorable au développement d'habitats coralliens et pourraient indirectement aider à prédire la distribution de ces habitats. Cette étude a fourni les bases scientifiques à la création d'un réseau Natura 2000 pour la préservation de l'habitat récif. Elle souligne également le besoin de connaissance, et éventuellement de stratégies de conservation, des habitats coralliens sur substrat meuble qui ne relèvent pas de la directive Habitat.

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Cold-Water Coral Habitats in Submarine Canyons of the Bay of Biscay

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The topographical and hydrological complexity of submarine canyons, coupled with high substratum heterogeneity, make them ideal environments for cold-water coral (CWC) habitats. These habitats, including reefs, are thought to provide important functions for many organisms. The canyons incising the continental slope of the Bay of Biscay have distinct morphological differences from the north to the south. CWCs have been reported from this basin in the late nineteenth century; however, little is known about their present-day distribution, diversity and environmental drivers in the canyons. In this study, the characteristics and distribution of CWC habitats in the submarine canyons of the Bay of Biscay are investigated. Twenty-four canyons and three locations between adjacent canyons were sampled using a Remotely Operated Vehicle (ROV) or a towed camera system. Acquired images were annotated for habitat type (using the CoralFISH classification system), substrate cover and coral identification. Furthermore, the influence of hydrological factors and geomorphology on the CWC distribution was investigated. Eleven coral habitats, formed by 62 morphotypes of scleractinians, gorgonians, antipatharians and seapens, inhabiting hard and/or soft substrate, were observed. The distribution patterns were heterogeneous at regional and local scales; the south Bay of Biscay and the southeastern flank favored soft substrate habitats. Biogenic and hard substrate habitats supported higher coral diversities than soft substrate habitats and had similar species compositions. A higher coral species turnover characterized soft substrate habitats. Substrate type was the most important driver of the patterns in both distribution and composition. Observations of coral reefs on steeper areas in the canyons and coral rubble on flatter areas on the interfluvial/upper slope support the hypothesis that canyons serve as refuges, being less accessible to trawling, although natural causes may also contribute to the explanation of this distribution pattern. The results of this study fed into a proposal of a Natura 2000 network in the Bay of Biscay where management plans are rare.

Keywords: cold-water corals, habitats, submarine canyons, Bay of Biscay, NE Atlantic, ROV, towed camera, distribution

INTRODUCTION

Submarine canyons incise many continental shelves and slopes around the world (Harris and Whiteway, 2011). These physiographical features have a complex, heterogeneous topography that creates specific hydrological processes, such as accelerated (bottom) currents, internal waves and dense shelf water cascading (De Leo et al., 2010; Harris and Whiteway, 2011). These processes have an influence on the sediment accumulation within canyons and are thought to transport organic matter from the continental shelf to the deep sea and to increase the suspended particulate matter concentration (De Leo et al., 2010; Harris and Whiteway, 2011). Internal waves enhance the mixing of water masses and the release of nutrients which in turn favor the development of plankton (Pingree and Mardell, 1985; Huthnance, 1995; Khripounoff et al., 2014). This primary production will be transported into the canyons, increasing the amount and quality of food (Huthnance, 1995; Amaro et al., 2015, 2016).

Because of the heterogeneous topography, including exposed hard and steep substrate, and the hydrological patterns, submarine canyons are hypothesized as biodiversity hotspots of cold-water corals (CWCs) (Mortensen and Buhl-Mortensen, 2005; White et al., 2005; Orejas et al., 2009; De Leo et al., 2010), compared to adjacent slope areas (Vetter et al., 2010; Cunha et al., 2011). CWCs are defined organisms belonging to the cnidarian classes Anthozoa and Hydrozoa that produce either calcium carbonate or black, horn-like, proteinaceous skeleton elements (Cairns, 2007). The orders that meet this definition are Scleractinia (stony corals), Alcyonacea (soft corals, including gorgonians), Antipatharia (black corals), Pennatulacea (seapens) as well as the hydrozoan family Stylasteridae (hydrocorals) (Cairns, 2007). Most of these CWCs need hard substrate to settle, with the exception of most seapens, some scleractinians (predominantly solitary) and some gorgonian species (Roberts et al., 2009). CWCs are filter-feeders that rely on currents to deliver food particles (Wagner et al., 2012) and vertical migration of zooplankton (Carrier et al., 2009; Mienis et al., 2012; Wagner et al., 2012; Hebbeln et al., 2014).

The scleractinians *Lophelia pertusa* and *Madrepora oculata* can form reefs (Roberts et al., 2006), which function as refuges, feeding areas and nurseries for many species, including commercially important fish (Roberts et al., 2006). CWC reefs are also linked to a high biodiversity (Freiwald et al., 2004; Roberts et al., 2009). While antipatharians, gorgonians and seapens cannot form reefs, they can occur in dense aggregations (coral gardens) and may provide similar functions as reefs (Roberts et al., 2006; Buhl-Mortensen et al., 2010; Baillon et al., 2012), for example, rockfish association with gorgonians in canyons of the Bering Sea (Miller et al., 2012).

Deep-water scleractinians occur mainly between 50 and 1,000 m water depth and in water temperatures of 4°–10°C (Roberts et al., 2006), occurring in a narrow density envelope of sigma-theta 27.35–27.65 kg/m³ as proposed by Dullo et al. (2008) for the North-East Atlantic that is linked to trophic inputs. Antipatharians and seapens can occur much deeper, even greater than 6,000 m (Williams, 2011; Wagner et al., 2012). The occurrence, abundance and diversity of CWC species and/or

habitat were influenced by temperature, salinity, water density, currents and trophic input (e.g., Roberts et al., 2006; Dullo et al., 2008; Yesson et al., 2012, in press; Mohn et al., 2014; Robert et al., 2015). Terrain parameters can be extracted from multibeam bathymetry and can serve as useful surrogates for habitat mapping. Slope, rugosity and Bathymetric Position Index (BPI) are examples of parameters measuring canyon topography and are known to have an influence on the presence of CWC species/habitats (e.g., Howell et al., 2011; Yesson et al., 2012; Robert et al., 2015).

CWCs are long-lived, have slow growth rates, form important structural habitats and are vulnerable to human activities, such as the fishing and oil and gas industries (Roberts et al., 2006; Ramirez-Llodra et al., 2011). Thus, CWC habitats meet the criteria of both VMEs (Vulnerable Marine Ecosystems; FAO) and EBSAs (Ecologically or Biologically Significant Marine Areas; CBD). As such, CWCs and their habitats have been listed as threatened or endangered by international organizations (OSPAR, ICES, Habitats Directives). Canyons are seen as natural refuges for these CWC habitats as well as other habitats, such as oyster banks (Van Rooij et al., 2010; Huvenne et al., 2011; Fernandez-Arcaya et al., 2017). Mapping and understanding the distribution of CWC habitats is, therefore, needed for conservation management along European margins. As a result of the importance of this part of the NE Atlantic as an integral sector or transition zone of this margin (Reveillaud et al., 2008; De Mol et al., 2011), the Bay of Biscay could potentially play a large role in persistence of those ecosystems on a global scale and, thus, potentially important for the connectivity between regions.

Habitat maps are becoming increasingly used in marine management and conservation. Areas selected for marine management and conservation can have different spatial scales, ranging from a particular zone or geographical feature, e.g., canyons or carbonate mounds, to an Exclusive Economic Zone (EEZ) of a country or areas as large as the North-east Atlantic. Classification systems aid in creating comprehensive, detailed and integrative habitat maps. An important advantage of classification systems is that they permit the use of a standardized terminology and habitat type over a large region. Classification systems may have different information or concepts, e.g., region, seascape, and biotope, depending on the goal of the marine management plan (Costello, 2009). A hierarchical system allows mapping of habitats at different scales, using a variety of data, depending on availability (e.g., different resolutions, quality, etc.); and can be adjusted to the needs and goals of the user (Costello, 2009).

A classification system comprising coral biota was developed during the EC FP7-funded project CoralFISH (Davies et al., in press). This classification system enables the comparison of coral habitats between regions in the NE Atlantic and Mediterranean using standardized terms and methods. It is a hierarchical system including biotopes (or habitats) formed by the dominant coral group(s)/species, dominant substrate type and potential geoforms, such as boulders and vertical walls (Davies et al., in press).

The continental margin of the Bay of Biscay, studied here, is incised by more than a 100 canyons and are organized into

drainage basins (Bourillet et al., 2003). Eight drainage basins occur from the Goban Spur to the Capbreton Canyon (Bourillet et al., 2006). Scleractinians were first reported in the Bay of Biscay in the late nineteenth century (e.g., Roule, 1896). However, the first maps of scleractinian occurrences were produced in the following century: Joubin (1922) used fishermen reports on scleractinians causing damage to demersal trawls and Le Danois (1948) mapped coral reefs along the continental slope of the Bay. Despite this early discovery, only a few CWC studies had been undertaken in the French part of the Bay of Biscay (Zibrowius, 1980; Reveillaud et al., 2008; De Mol et al., 2011) and the largest part of this basin still remains unexplored.

Here, we report investigations of the presence of CWC habitats in the submarine canyons of the Bay of Biscay based on surveys using a Remotely Operated Vehicle (ROV) and a towed camera system. The CoralFISH coral biota classification system was used to delimit coral habitats. The goals of this study were: (i) to identify coral habitats in the canyons of the Bay of Biscay, (ii) to identify coral species and their abundances, densities and diversities within these habitats and their compositions, (iii) to investigate the distribution of coral

habitats in the Bay of Biscay, and (iv) to explore the influence of other environmental factors (temperature, water density, depth, derivatives of the bathymetry) and geomorphology on the presence and distribution of coral habitats.

MATERIALS AND METHODS

Study Site

Margin Morphology

The Bay of Biscay is part of the North-East Atlantic Ocean, located west of France and north of Spain. It is a passive margin containing three parts; the Celtic, Armorican and Aquitaine margins (Zaragosi et al., 2000). Within this study, the Bay of Biscay was defined using geological boundaries (see Bourillet et al., 2006) therefore including all three margins, as the Celtic margin is part of the Celtic Sea according to hydrographical terms.

The morphology of the Celtic and the Armorican margins (Figure 1), limited by the Goban Spur in the north and the Conti spur in the south, is characterized by spurs and canyons (Bourillet et al., 2006). The continental shelf is wide, up to 200

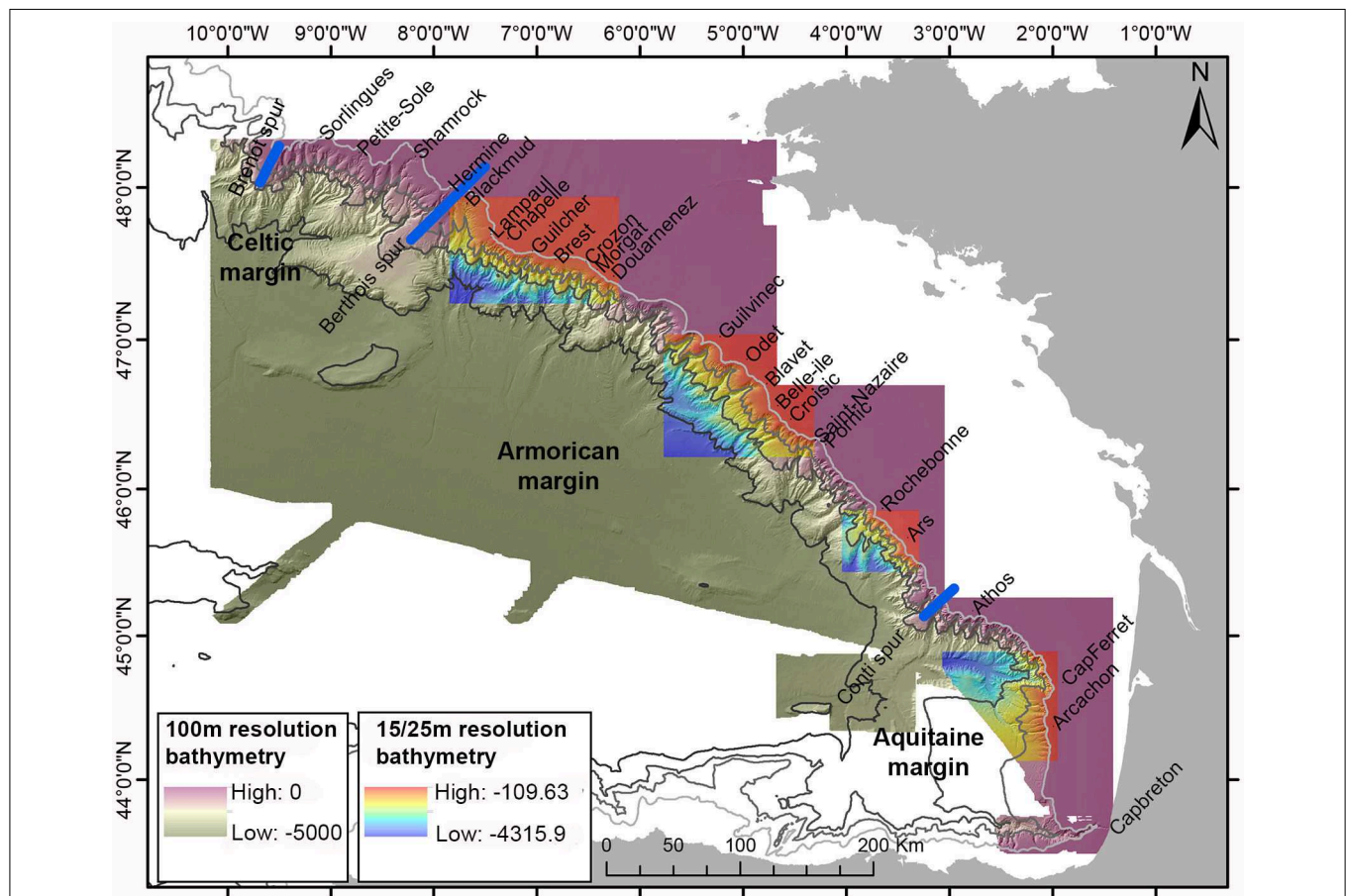


FIGURE 1 | A map of the submarine canyons incising the continental slope of the Bay of Biscay. The bathymetry is available at a 100 m resolution for the whole Bay of Biscay (green-purple) and at a 15/25 m resolution for four boxes representing each zone (rainbow-colored) from Bourillet et al. (2012). The blue lines indicate the Brenot, Berthois and Conti spurs, dividing the margin into the Celtic, Armorican and Aquitaine margins.

km for the Armorican margin and more than 250 km for the Celtic margin (Bourillet et al., 2006). These two margins can be divided into three zones based on the geomorphology of the continental margins, the influences of sedimentation and hydrodynamic regimes (**Figure 1**): (i) the Celtic and northern Armorican margin, (ii) the central Armorican margin, and (iii) the southern Armorican margin.

The morphology of the first zone—the Celtic and northern Armorican margins—is complex and comprises some shelf-incising submarine canyons (**Figure 1**). These canyons contain several morphological features, such as cliffs, mainly formed in the head of the canyons by regressive erosion from the bottom to the top of the canyon (Bourillet et al., 2010). There are three main deep-sea drainage systems: (i) the Petite Sole drainage basin on the Celtic margin, comprising the canyons from Sorlingues to Hermine, (ii) the Chapelle drainage basin, comprising the canyons from Blackmud to Guilcher, (Bourillet and Lericolais, 2003) and, (iii) the West Brittany drainage basin, comprising the canyons from Brest to Douarnenez (Zaragosi et al., 2000, 2001). Zone 1 is under the influence of tidal currents of the English Channel (Zaragosi et al., 2001) and is linked with the drainage basins of rivers, such as the Seine, via the Channel paleo-river (Bourillet et al., 2003).

The second zone is the central part of the Armorican margin (**Figure 1**). This zone includes an alternation of large and narrow canyons. The large canyons, considered to be formed first, cut the continental shelf, while the heads of the narrow canyons, formed during a later stage, are located halfway down the slope (Bourillet et al., 2010). Two drainage systems are found within this part of the Armorican shelf: (i) the South Brittany drainage system, including the canyons from Audierne, south of Douarnenez Canyon, to Blavet Canyons (Zaragosi et al., 2001), and (ii) the Gascogne drainage system from the Belle-île to Yeu Canyons (also including Croisic, Saint-Nazaire and Pornic Canyons) (Bourillet et al., 2006). These canyons are not under the influence of the English Channel any longer and sediment is transported from the continental shelf to these canyons (Zaragosi et al., 2001).

The third zone comprises the southern part of the Armorican margin (**Figure 1**). Even though canyons still reach the continental shelf in this part of the Bay of Biscay, they are smoother than those on the Celtic and northern Armorican margins. The flanks of the canyons in this zone are regular and sedimentary, while the thalwegs are continuous with sloping banks. Cliffs are either scarce or not present in this zone (Bourillet et al., 2010). The Rochebonne drainage basin, comprising the canyons from Sables d'Olonnes, north of Rochebonne Canyon, to Oleron Canyon, north of the Conti Spur, is the only drainage system within this zone (Bourillet et al., 2006) and includes Rochebonne and Ars Canyons.

The third margin of the Bay of Biscay, the Aquitaine margin, from the Conti Spur to Capbreton Canyon, can be considered as a fourth zone of the Bay of Biscay (**Figure 1**). The continental shelf is narrow, with only 70 km from the shore (Bourillet et al., 2006). The continental slope of this margin is a “tectonic-dominated” margin instead of a “canyon-dominated” slope (Bourillet et al., 2006). The dominant relief, the Landes plateau, is surrounded

by two major canyons: Cap-Ferret and Capbreton. The “gouf de Capbreton” is an exceptional example of a shelf-incising canyon with a head close to the beach and a very gentle along-slope profile (Cirac et al., 2001; Bourillet et al., 2007). The flanks of the canyons on this margin have a weak slope and they do not present steps or cliffs. The Cap-Ferret and Arcachon thalwegs are broader than those of other canyons, north of this zone/margin (Bourillet, 2010; De Chambure et al., 2013).

Water Masses and Currents

In the Bay of Biscay several water masses with different origins and densities can be found (de Madron et al., 1999; van Aken, 2000a,b): (i) the Eastern North Atlantic Water (ENAW), (ii) the Mediterranean Outflow Water (MOW), (iii) the Labrador Sea Water (LSW), and (iv) the Northeast Atlantic Deep Water (NEADW). The ENAW is usually found between 200 and 600 m water depth. It originates from the Labrador Current and may contain a significant amount of Antarctic Intermediate Water (AAIW) transported to the NE Atlantic by the Gulfstream-North Atlantic Current. The more saline and denser MOW is deeper and generally flows between 700 and 1,300 m water depth. This water mass is more pronounced in the south of the Bay of Biscay and becomes less noticeable in the north of the Bay of Biscay toward Porcupine Seabight. The third water mass is the LSW and reaches to ~2,000 m depth. It is usually mixed with the MOW by internal waves near the continental slope and therefore this water mass is less apparent. The fourth and last layer is the NEADW originating from multiple water masses, including MOW and LSW. It occurs approximately between 2,000 and 2,600 m water depth.

There are several currents and other hydrological processes occurring in the Bay of Biscay that modify the temperature, salinity and density of the water masses. The slope current runs along the continental slope of the Bay of Biscay. It arrives in this basin via the Portuguese and Spanish continental slopes (Pingree and Le Cann, 1989, 1992; Koutsikopoulos and Le Cann, 1996) and is thought to be a density driven current formed by the MOW (Pingree and Le Cann, 1989). Even though the slope current is influenced by the complex morphology of the continental slope, it moves dominantly northwards/polewards (Pingree and Le Cann, 1989, 1992; Koutsikopoulos and Le Cann, 1996).

Other important processes in canyons of the Bay of Biscay are tidal currents and internal waves (Koutsikopoulos and Le Cann, 1996; Mulder et al., 2012). Tidal currents can have speeds up to 1 m/s (de Madron et al., 1999; Mulder et al., 2012; Khrpounoff et al., 2014) and are weaker in the southern region of the Bay of Biscay (lower than 45°N) (Koutsikopoulos and Le Cann, 1996). These currents follow a semi-diurnal tidal frequency (e.g., Pingree and Le Cann, 1989; Koutsikopoulos and Le Cann, 1996; de Madron et al., 1999; Mulder et al., 2012) and can extend deep into the canyons (Pichon et al., 2013). Internal waves cause the resuspension of sediment and create nepheloid layers, as observed in Cap-Ferret Canyon on the Aquitaine margin (de Madron et al., 1999).

Currents have an influence on the primary production or on other biological traits within the Bay of Biscay. Tidal currents and upwelling are thought to promote water mixing and the

release of nutrients. This creates a favorable environment for phytoplankton growth, thus enhancing primary production (Pingree and Mardell, 1985; Huthnance, 1995). Tidal currents and internal waves can transport the primary production into canyons, thus providing food for filter-feeders such as CWCs (Huthnance, 1995; Amaro et al., 2015, 2016).

Data Collection

Data were collected during seven cruises on the R/V *Pourquoi Pas?* the R/V *Le Suroît* and the R/V *Thalassa* between 2009 and 2012 (Table 1). The BobGeo, BobGeo 2 (Bourillet, 2009, 2010) and BobEco (Arnaud-Haond, 2011; Arnaud-Haond and Grehan, 2011) cruises were performed under the European FP7-funded project CoralFISH. This project “assesses the interaction between CWCs, fish and fisheries, in order to develop monitoring and predictive modeling tools for ecosystem based management in the deep waters of Europe and beyond” (<http://eu-fp7-coralfish.net/>). The main objectives of these cruises were the exploration for, and study of geological features and/or marine ecosystems, with a specific focus on scleractinian coral habitats in the canyons of the Bay of Biscay. The Evhoe cruises were resource surveys targeting the evaluation of fish stocks in the Bay of Biscay for multiple utilizations, e.g., stock evaluation models. Data acquired using a towed camera system (see below) on these cruises were utilized to explore the benthic communities in canyons.

In total, 46 dives using an ROV or a towed camera were undertaken: 43 dives within 24 canyons and 3 additional dives on interfluvies or on the upper slope between adjacent canyons (Table 2). The latter dives were difficult to assign to either one of these two canyons; the name of both canyons were therefore used and they were, thus, treated separately (interfluvie: dive BE_480 between Morgat and Douarnenez; upper slope: dive BG2_05 between Odet and Guilvinec and dive BG1_08 between Odet and Blavet Canyons; Table 2). Most canyons were named, except for the canyon north of Éperon Ostrea; to simplify the reference to this particular canyon, the term/name “La Chapelle” was used, named after “le haut-fond de La Chapelle,” an area of sand waves on the continental shelf near the head of this canyon.

A towed camera system, Scampi, was used to collect images during 33 dives performed on six cruises included in this study (Table 1). The frame was fitted with a Nikon D700 stills camera directed vertically downwards. The camera was towed ~2–3 m

above the seafloor and photos were manually taken at intervals of ~10–90 s.

During the BobEco cruise, image footage for 13 dives was acquired using the ROV Victor6000 (Table 1). The ROV was equipped with multiple cameras, of which the vertically directed video camera was used within this study (Sony FCB-H11). Frame-grabs from the videos were taken at 1-min intervals using the ADELIE annotation software (Ifremer, www.ifremer.fr/adelie) to allow comparison between the ROV image footage with photos taken by the Scampi system; both frame-grabs and photos are called “images” hereafter.

Metadata, such as the navigation data and the timecodes of the videos/photos were extracted using ADELIE. A USBL system (Ultra-Short BaseLine system) was used for accurate positioning of the vehicles, but was unavailable for all Evhoe-cruises, so the ship navigation was used for these dives.

Image Analysis

Each image was subjected to a quality control prior to analysis, based on three criteria: (i) altitude; images were included if they were taken between 1 and 5 m from the seafloor, (ii) image quality; poor quality images due to sediment clouds obscuring the image, the image being out of focus or taken in low light-conditions, were removed before analysis, and (iii) vehicle movement; images were excluded during stationary phases (ROV only).

Images that passed the quality control were annotated for (i) habitat type, (ii) substrate cover (subset; see below), and (iii) fauna (subset; see below).

Habitat Type

Habitat type was visually assigned for images based on the coral biota classification system created within the CoralFISH project (Davies et al., in press). This classification system was created as a tool to standardize habitat observations across the CoralFISH regions in the North-east Atlantic and Mediterranean. The definition of a habitat given by this classification was an area “where a coherent suite of conspicuous epibenthic organisms, including CWCs, extending throughout a minimum estimated area of 25 m² as observed by underwater cameras.” Coral biotopes (or habitats) were based on the dominant coral species or group of species, the presence of scleractinian framework, usually *L. pertusa* and *M. oculata*, and the substrate type. Large

TABLE 1 | Dive information including cruise name, year, ship, the optical technique that is used and the number of dives analyzed during this study.

Cruise	Cruise-code	Year	Ship	Optical technique	Number of dives
BobGeo	BG1	2009	R/V <i>Pourquoi Pas?</i>	Scampi	11
Evhoe 2009	EVH09	2009	R/V <i>Thalassa</i>	Scampi	3
BobGeo 2	BG2	2010	R/V <i>Le Suroît</i>	Scampi	6
Evhoe 2010	EVH10	2010	R/V <i>Thalassa</i>	Scampi	4
BobEco	BE	2011	R/V <i>Pourquoi Pas?</i>	ROV	13
Evhoe 2011	EVH11	2011	R/V <i>Thalassa</i>	Scampi	3
Evhoe 2012	EVH12	2012	R/V <i>Thalassa</i>	Scampi	6

Cruises are arranged in a chronological order.

TABLE 2 | Description of the dives used to collect the image footage, including the margin of the Bay of Biscay, the number of images (total and analyzed), the location within the canyon (NW flank, north-western flank; SE flank, south-eastern flank) and the presence of coral habitat.

Canyon	Dive code	Latitude	Longitude	Margin	3D-length (km)	Min depth (m)	Max depth (m)	No. images total	No. images analyzed	Location in canyon	Presence coral habitat
Sorlingues	BE_472	48.1218030	−9.1480668	Celtic	3.4	1,066.4	2,323.0	271	168	SE flank	Yes
	BE_477	48.1783925	−9.0844680	Celtic	9.3	375.7	1,232.1	709	587	NW flank	Yes
	EVH12_9	48.2265612	−9.2667409	Celtic	4.4	232.4	858.4	611	360	NW flank	Yes
Petite-Sole	BE_471	48.1368207	−8.8111888	Celtic	8.2	674.6	989.7	527	452	NW flank	Yes
	BE_476	48.1201765	−8.8119502	Celtic	2.7	939.5	959.3	241	191	NW flank	Yes
	EVH09_3	48.1317020	−8.8065981	Celtic	3.4	654.1	986.6	747	691	NW flank	Yes
Shamrock	EVH09_1	48.1623919	−8.4591893	Celtic	4.8	185.5	199.9	299	299	Upper slope	No
	EVH09_2	48.1462677	−8.4910439	Celtic	1.1	199.9	213.0	113	111	SE flank Upper slope	No
	EVH12_8	48.0753351	−8.3109878	Celtic	3.8	585.0	1,126.4	666	480	SE flank	Yes
Hermine	EVH10_3	47.8661239	−8.0250322	Celtic	3.3	387.9	1,344.4	268	230	NW flank	Yes
	EVH10_4	47.8277152	−8.1472261	Celtic	2.4	1,029.4	1,854.4	215	195	NW flank	Yes
Blackmud	EVH11_4	47.8193228	−7.6824182	North Armorican	5.3	557.6	1,223.1	712	671	SE flank	Yes
Lampaul	BE_470	47.5633329	−7.5321780	North Armorican	11.9	1,069.3	2,665.5	1,092	626	NW flank Thalweg	Yes
	BE_478	47.6230440	−7.5284670	North Armorican	9.4	506.8	1,245.1	891	500	SE flank NW flank	Yes
La Chapelle* (north of épiron Ostrea)	BG1_1	47.5972543	−7.3018781	North Armorican	1.6	224.7	352.3	103	92	SE flank Upper slope	No
	BG1_2	47.5689723	−7.3459289	North Armorican	2.9	417.4	1,076.0	193	154	SE flank	Yes
	BG1_3	47.5898404	−7.3593201	North Armorican	0.4	439.2	546.2	21	19	NW flank	No
	BG1_4	47.5771639	−7.3609736	North Armorican	1.6	574.9	1,039.0	111	97	NW flank	Yes
Guilcher	EVH11_3	47.5076895	−7.1311674	North Armorican	4.8	437.6	1,647.9	694	673	NW flank	Yes
Brest	EVH12_7	47.4702872	−6.8970797	North Armorican	4.1	451.6	1,480.5	593	429	NW flank	Yes
Crozon	BE_479	47.3877187	−6.6237915	North Armorican	10.3	692.4	1,382.0	577	491	NW flank	Yes
Morgat	BG1_5	47.3881001	−6.4512668	North Armorican	3.7	421.3	1,200.4	310	280	SE flank Upper slope	Yes
	BG1_6	47.3647983	−6.4366369	North Armorican	0.8	580.2	854.8	94	79	NW flank	Yes
Morgat-Douarnenez	BE_480	47.3061795	−6.3521557	North Armorican	8.9	713.9	1,204.1	491	386	NW flank	Yes
Douarnenez	EVH11_2	47.3191960	−6.2723000	North Armorican	4.0	559.0	1,577.9	622	594	SE flank	Yes
Guilvinec	BE_469	46.9327758	−5.3597874	Central Armorican	4.9	803.9	953.2	624	294	NW flank	Yes

(Continued)

TABLE 2 | Continued

Canyon	Dive code	Latitude	Longitude	Margin	3D-length (km)	Min depth (m)	Max depth (m)	No. images total	No. images analyzed	Location in canyon	Presence coral habitat
Odet-Guilvinec	BG2_5	46.8720076	−5.2427669	Central Armorican	0.7	227.5	229.9	61	54	Upper slope	Yes
Odet	BG1_7	46.7841307	−5.1649952	Central Armorican	2.7	649.0	1,309.3	243	187	NW flank	Yes
	BG1_9	46.7880887	−5.0518116	Central Armorican	2.0	550.4	952.5	167	140	SE flank	No
	BG1_10	46.7803604	−5.2221504	Central Armorican	1.3	631.4	898.5	94	83	NW flank	Yes
	BG2_6	46.8271589	−5.2687434	Central Armorican	5.7	349.9	1,170.5	370	352	SE flank	Yes
	EVH10_2	46.8149943	−5.1739369	Central Armorican	2.5	250.1	484.0	209	187	NW flank	No
Odet-Blavet	BG1_8	46.7400293	−5.0418340	Central Armorican	2.6	292.4	396.5	215	173	Upper slope	No
Blavet	EVH10_1	46.6301345	−4.8558125	Central Armorican	5.8	280.5	410.5	356	334	SE flank Upper slope	Yes
Belle-île	BG1_11	46.4822928	−4.7384651	Central Armorican	2.1	427.0	984.0	151	143	SE flank	Yes
Croisic	BE_468	46.3814420	−4.6793497	Central Armorican	4.1	708.9	1,050.7	337	244	SE flank	Yes
St. Nazaire	BE_467	46.2535308	−4.4086068	Central Armorican	2.6	1,130.4	1,761.8	296	126	NW flank Thalweg	Yes
Pornic	EVH12_5	46.2346696	−4.3360429	Central Armorican	3.3	598.7	1,329.7	752	693	SE flank	Yes
Rochebonne	BE_465	45.7780478	−3.7746150	South Armorican	3.6	580.0	1,487.4	295	134	NW flank	Yes
Ars	BE_466	45.6798080	−3.6225145	South Armorican	3.0	518.3	1,130.8	307	171	NW flank	Yes
	BG2_1	45.6471834	−3.5535464	South Armorican	3.6	470.4	1,192.3	216	207	SE flank	Yes
Athos	EVH12_4	45.0544300	−2.8789364	Aquitaine	10.3	309.0	2,539.2	1,119	1,001	Thalweg NW flank Upper slope	Yes
Cap-Ferret	EVH12_3	44.7941036	−2.2029170	Aquitaine	7.5	523.0	1,913.5	1,250	1,098	NW flank	Yes
Arcachon	BG2_2	44.3973083	−2.4176186	Aquitaine	2.7	1,103.7	1,533.6	159	151	NW flank Thalweg	Yes
	BG2_3	44.3717064	−2.4282195	Aquitaine	1.2	1,261.9	1,516.0	83	76	SE flank Thalweg	Yes
	BG2_4	44.3298353	−2.2306230	Aquitaine	3.8	768.1	1,085.0	184	171	NW flank Thalweg SE flank	Yes

*The canyon where these dives were performed, north of the Épiron Ostrea, does not have a name. "La Chapelle" is used to refer to this canyon, using the same term as the sandbank on the continental shelf near this canyon.

geological features, such as vertical walls and boulders, were also included in the classification.

The CoralFISH coral biota classification system is a hierarchical system consisting of three levels (Davies et al., in press): level 1, the broadest level, includes the dominant of coral type(s) and substrate type, whereas level 3, the most detailed level, includes the coral species constructing the habitat, the substrate type and possible geological features as well as conspicuous non-coral species. Due to the large variation and thus the high number of level 3 habitats over a large study area, only the first level of this classification was used (Biotope level 1).

Substrate Cover and Fauna

Substrate cover and fauna were analyzed on a subset (2,350 images) of the 4,191 images on which CWC habitats were observed (see Section Results). The subset was created by selecting images at an interval of ~1 min from the beginning of the dive. As the images acquired using the Scampi system were taken manually and at irregular intervals, images taken 15 s before or after the 1-min interval were considered for the subset.

Substrate cover, including colonial scleractinians, was measured using a 100 point grid, which was placed over the subset images using the software COVER (C. Carré, Ifremer; see Gomes-Pereira et al., 2016). Substrate types were assigned to each point and a relative substrate percentage cover of the visible part of the image was calculated for each subset image.

For each subset image, fauna were enumerated and identified to the lowest taxonomic level possible. It is difficult to identify deep-sea species to species level from images, because of a lack of associated identifications based on morphological characteristics or genetics. Therefore, they were identified as morphotypes and given an Operational Taxonomic Unit (OTU). To aid identification, a species catalog was used (Howell and Davies, 2010: <http://www.marlin.ac.uk/deep-sea-species-image-catalogue/>) and updated as part of a collaborative project between Plymouth University, Ifremer and NOAA. For this current study, the focus was coral morphotypes. Where possible, species were identified and/or confirmed by coral taxonomists using voucher-specimen collected during the BobEco cruise (see Acknowledgments).

For the reef-forming scleractinian species *L. pertusa*, *M. oculata*, and *Solenosmilia variabilis* percentage cover was measured using the same method as substrate cover. These three species were not included in any result concerning the abundances of individual organisms. However, they were included in a number of analyses (see Section Statistical Analysis). In many instances, the resolution of images did not allow for discrimination between *L. pertusa* and *M. oculata*, therefore were treated as one morphotype, since previous literature has shown that these species nearly systematically co-occur in the Bay of Biscay (De Mol et al., 2011; Arnaud-Haond et al., in press).

Habitat Segments

In order to assess the length of CWC habitats, their taxonomic composition and environmental characteristics, habitat segments were defined as all the adjacent images showing the same habitat,

until another habitat was assigned to an image. The lengths (hereafter “linear”) of both habitat segments and dives were measured in 3D using ArcGIS (Table 2).

Environmental Data

Bathymetry and Derivatives

A digital Terrain Model (DTM) was available for the whole Bay of Biscay at a resolution of 100 m (Figure 1). DTMs were also available for four boxes (bob-boxes) at a higher resolution of 15 or 25 m (Bourillet et al., 2012), representing each of the four zones of the Bay of Biscay (Figure 1; Section Margin Morphology). The boxes Bob-1 and Bob-2 have a surface of ~10,000 km² and are located on the northern and central part of the Armorican margin, respectively. The third box, Bob-3, has a surface of ~1,900 km² and represents the southern part of the Armorican margin. The fourth box, Bob-4, with a surface of ~7,000 km², is located on the Aquitaine margin. The resolutions of Bob-1, Bob-3, and Bob-4 are 15 m, however, the resolution of the Bob-2 bathymetry is lower (25 m), due to poor weather conditions during the time of acquisition. The bathymetry for the dives on the Celtic margin and Athos Canyon (Aquitaine margin) was only available at the lower (100 m) resolution. For the consistency across the whole dataset, depth-values were extracted from the lower (100 m) bathymetry resolution. This resolution was also used to measure the 3D-length of the dives and habitat segments.

Terrain derivatives were extracted from the bathymetry using the ArcGIS extension Benthic Terrain Modeler v. 3.0 (Wright et al., 2012). Slope, direction (northness or cosAspect, eastness or sinAspect), curvature (general, plan and profile), Surface to Planar, BPI and a measure of rugosity (VRM = Vector Ruggedness Measure) were calculated. Neighborhood sizes of ~200, 300, and 500 m were chosen for the fine scale BPI and 1 and 1.5 km for the broad scale BPI. For the VRM, similar neighborhood sizes (except 200 m) were used.

Geomorphology

Geomorphological classes were produced for the entire Bay of Biscay, using bathymetry data, its derivatives, such as slope, canyon network extraction as well as expert interpretation (De Chambure et al., 2013). The geomorphological classes are available on the same resolutions as the DTMs and mapped by Bourillet et al. (2012) and are using the Coastal and Marine Ecological Classification Standard (CMECS) code (Madden et al., 2008). A total of 21 classes have been created on the higher (15/25 m) resolution for the bob-boxes and 15 classes on the lower (100 m) resolution for the whole Bay of Biscay.

One of 15 geomorphological classes at a 100 m resolution was attributed to each image for the whole dataset in ArcGIS 10.2 and one of 21 classes at a 15/25 m resolution for each image in the bob-boxes. Due to the uneven and sometimes low number of images per geomorphological class, classes were merged for statistical robustness according to three different criteria: (i) Morphology with three attributes: Canyon, Interfluvial and Upper slope, (ii) Slope, with four intervals depending on the resolution: at 15 m resolution: <10°, 10–20°, 20–40°, and >40°; at 100 m resolution: <10°, 10–15°, 15–25°, and >25°, and (iii) Location,

with two attributes: northwestern and southeastern flank of a canyon/interfluvium (Table 2).

Temperature, Salinity, and Water Density

Seawater potential temperature and salinity data were publicly available (Copernicus Marine Environment Monitoring Service: <http://marine.copernicus.eu/>) at a resolution of 0.083° latitude (~10 km). These variables were available for different depth layers (from 0 to 5,500 m depth). The monthly means from 15/12/2009 to 15/12/2011, available at the lowest depth layer as possible, were used to calculate mean potential temperature (in Kelvin) and salinity (in PSU). A geotiff (geo-referenced image) was created for both variables and a value extracted for each image of the data set in ArcGIS. Temperature values were transformed to °C.

The seawater density can describe the mixing of water masses. The potential density anomaly (sigma-theta or σ_θ), using the potential temperature instead of *in situ* measured data, was calculated according to Dullo et al. (2008).

A raster of the sigma-theta was calculated using the rasters of the potential temperature and salinity data in the software program R. A value was extracted for each image using ArcGIS from a geotiff.

Statistical Analysis

Coral Community and Composition

Several metrics—abundance, density and diversity—were used to characterize the habitats and the engineering coral species. Mean coral densities per habitat type and per segment were calculated. The density was expressed per image, instead of per linear transect or surface measure for three reasons: (i) only a subset of images were analyzed for fauna which makes it difficult to give densities per linear meter, (ii) no lasers were available on both optical techniques, and (iii) the altimeter on the Scampi frame was not reliable enough to give good estimations of area of images, complicating the expression of densities by surface measure. A spearman correlation was calculated to investigate whether segment length and mean densities (in individuals/image) per segment were correlated.

Rarefaction analysis (individual based) was used to compare differences in richness of corals between habitats. The Hurlbert's index (Hurlbert, 1971) is given as a diversity index, comparing the diversity of the habitats using a random sample size equal to the smallest number of individuals observed in one of these habitat, and thus, limiting the influence of unequal sample sizes. The three scleractinians measured as percentage cover were excluded from these analyses.

A Spearman correlation tested the relationship between the mean percentage of scleractinian cover and the total abundances of other coral types, i.e., antipatharians, gorgonians and seapens, per habitat segment.

Principal Component Analyses (PCA) were computed to investigate the (dis)similarities in species composition of the different habitats. Two PCAs were performed: (i) a PCA on a covariance matrix using the Hellinger-transformed abundances of each morphotype per habitat, excluding the reef-forming scleractinians *L. pertusa*, *M. oculata*, and *S. variabilis*, and (ii)

a PCA on a correlation matrix using the raw total abundances of morphotypes and the mean percentage scleractinian cover per habitat. The later included the three previous mentioned scleractinians. The Hellinger-transformation gives a low weight to the morphotypes with a high abundance (Legendre and Gallagher, 2001).

Habitat Distribution and Environmental Characteristics

Coral habitats were mapped in the canyons surveyed in the Bay of Biscay. The proportion of each coral habitat per canyon was used to describe the distribution of these habitats per canyon.

A PCA was computed to investigate the (dis)similarities in habitat types observed in the canyons using the Hellinger-transformed total linear (i.e., lengths) of each coral habitat (Legendre and Gallagher, 2001).

A specific principal component analysis with respect to instrumental variables, the Between-Class Analysis (BCA; Doledec and Chessel, 1987), was used to investigate if the habitats were characterized by different environmental settings. The BCA is a multivariate analysis which partitions and maximizes the variance between groups of one qualitative variable. A matrix of environmental variables (including latitude, temperature, sigma-theta, slope, northness, eastness, general, plan and profile curvature, Surface to Planar, BPI, and VRM) per habitat segment was used as the response variable and the habitats (all habitats separately or categorized into biogenic, hard substrate and soft substrate habitats) were used for partitioning. This analysis aims to discriminate the segments based on their environmental conditions and how much of this variation is explained by the habitats.

Chi-square tests were used to test for differences in coral distribution according to the three qualitative variables: morphology, slope and location. Chi-square tests were undertaken using the image data, rather than habitat segments because they involve the geomorphological classes (see Section Environmental Data) and habitat segments can cross geomorphological classes.

All analyses were performed using the open source software R. The R packages “ade4” (Dray and Dufour, 2007) and “vegan” (Oksanen et al., 2016) were used for the diversity measurements, PCAs and BCA.

RESULTS

Of the 14,874 analyzed images, coral habitats were recorded on 4,191 images, of which 2,350 images were selected for substrate cover measurements and species identification (“subset” images).

Substrate and Scleractinian Coral Framework Cover

Seven geological substrate types were encountered and divided into two main categories: (i) **hard substrate**, consisting of hardground/bedrock, hardground/bedrock covered by a (thin) layer of soft sediment, consolidated mud, boulders, pebbles and/or cobbles, and (ii) **soft substrate**, consisting of mud/sand and/or gravel.

Four **biogenic substrate** types were observed: live scleractinian framework, dead scleractinian framework, scleractinian coral rubble, and shell debris. Percentages of these categories were summed to obtain the percentage of total framework (live and dead) and total scleractinian cover (live and dead framework and rubble). Scleractinian framework and rubble included the reef-forming species (*L. pertusa*, *M. oculata*, and *S. variabilis*) as well as another colonial scleractinian *Enallopsammia rostrata*. *E. rostrata* occurred mostly, if not only, on vertical features, such as steps or walls, but did not form reefs or dense structures like the reef-forming scleractinians do. However, the cover of *E. rostrata* was included in the total scleractinian framework and the total cover, because of the three-dimensional structures they can form compared to solitary scleractinians that are usually only a few centimeters high.

Up to four substrate types were recorded for an image, although the seafloor was covered by either two or three substrates on most images.

Coral Habitats and Species

Eleven different coral habitats were observed (Figures 2A–J) using the CoralFISH classification: coral reef, coral rubble, colonial scleractinians on hard substrate, solitary scleractinians on hard substrate, antipatharians or gorgonians on hard substrate, mixed corals on hard substrate, colonial scleractinians on soft substrate, solitary corals on soft substrate, gorgonians on soft substrate, seapens on soft substrate and mixed corals on soft substrate. Hereafter, hard and soft substrate will be abbreviated as “HS” and “SS,” respectively, and will be used in combination with the structuring coral type to indicate the habitat. A description of each habitat is given in the (Supplementary Data S1) including their linear, their coral species composition and environmental settings.

The coral habitats were observed in total linears (or length; see Section Habitat Segments) from as little as 6 m to more than 10 km (Table 3). The most common habitat was coral rubble, with a linear of 18.1 km, equivalent to 10.1% of the total observed linear; followed by coral reef (linear: 10.7 km; 6.0% of the total observed linear). Both rubble and reef habitats were also observed on the highest number of segments (162 and 106 respectively). Seapens SS was the third most observed habitat (linear: 6.7 km; 3.8% of the total observed linear) and thereby the most common soft substrate habitat. Mixed corals SS was the habitat on soft substrate that was observed the least (linear: 365 m; 0.2% of the total observed linear) and the “solitary scleractinians HS” habitat was observed only once, with a linear of 6.0 m (less than 0.01% of the total observed linear). Due to this small contribution, this latter habitat was excluded from any analyses as none of the three images of this habitat was selected for the “subset” image dataset (Table 3).

Even though rubble and reef habitats had the longest total linear, these are mainly caused by a higher sample size and a few segments that were much longer than most segments. The median segment length of coral reef (65.3 m) was similar to the median segment lengths of seapens SS (64.3 m) and solitary scleractinians SS (62.4 m) (Table 3). Coral rubble has a smaller median segment (54.5 m; Table 3).

The Coral Assemblages

Community structure

A total of 6,287 individual corals were observed belonging to 59 coral morphotypes (Tables 3, 4). Including the three reef-forming scleractinian corals—*L. pertusa*, *M. oculata*, and *S. variabilis*—of which coverage was measured, instead of abundances, the total added up to 62 morphotypes. Thirty-four of these morphotypes were identified down to at least genus level. The most abundant morphotypes that could be counted, comprising together 53% of the coral individuals were the antipatharian *Leiopathes* spp. (2,089 individuals; 33.2%), the primnoid *Narella versluysi* (677 individuals; 10.8%) and the seapen *Kophobelemnion cf. stelliferum* (581 individuals; 9.2%) (Table 4). The soft coral suborder Alcyoniina (Alcyonacea) was observed the least with 17 individuals (0.3% of the total observed coral individuals) (Table 4).

The abundances, densities (individuals per image) and species richness varied according to the coral habitat types (Table 3). Abundance patterns between habitats did not strictly follow their sample size patterns. In particular, the most common habitat, coral rubble, had a low number of corals (672 individuals) relative to coral reef (3,208 individuals). Overall, the mean coral density within habitat segments did not correlate with the linear of the segments ($R = -0.003$, $p = 0.955$), suggesting that the size of the habitats did not influence the aggregation of corals. Mixed corals HS, antipatharians/gorgonians HS and coral reef achieved the top three highest coral densities (7.8, 6.8, and 5.3 individuals/image respectively). The highest densities on soft substrate habitats were half of those on hard substrate (solitary scleractinians SS: 3.6 individuals/image; seapens SS: 3.4 individuals/image). Similarly, the total number of morphotypes on hard substrate and biogenic habitats ranged from 21 to 32, of which coral reef and mixed coral HS are the most species rich (32 and 30 morphotypes respectively). The total number of morphotypes on soft substrate habitats ranged from 2 to 19, of which colonial scleractinians SS and seapens SS are the most species rich (19 and 12 morphotypes respectively).

Species accumulation curves showed that, with the exception of coral reef, seapens SS and mixed corals HS, habitats were undersampled as no curve reached an asymptote (Figure 3). Comparison of diversity values, even with indices limiting sampling biases, should, therefore, be taken cautiously. Some patterns, however, still stand out. The diversity of the soft substrate habitats formed by solitary scleractinians, gorgonians, seapens and a mix of these corals was very low compared to the coral habitats on hard substrate and the biogenic habitats, in line with the density and richness patterns (Figure 3; Table 3). A noticeable exception is the colonial scleractinians SS habitat, which diversity was similar to that of biogenic habitats. The two best characterized habitats, coral reef and seapens SS, shared a low equitability, as shown by the slope of the species accumulation curves. In the coral reef habitat, three morphotypes and a cluster of species were highly abundant, contributing to 84% of total abundance: the antipatharian *Leiopathes* spp. (1,923 individuals), the antipatharian *Stichopathes gravieri* (293 individuals) and the gorgonian *N. versluysi* (238 individuals) and unidentified

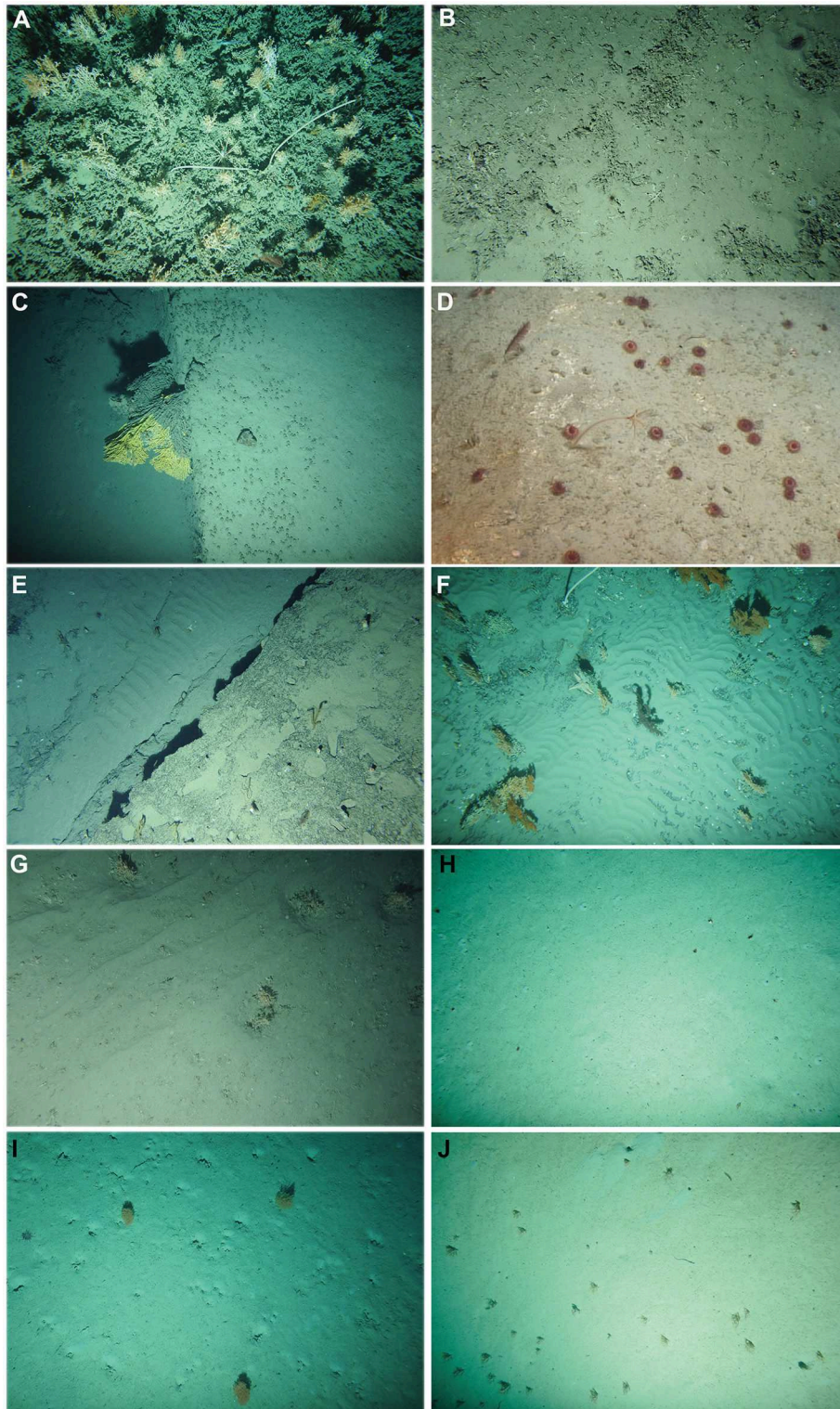


FIGURE 2 | Example images of the coral habitats of the Bay of Biscay: (A) Coral reef (BobGeo 2009), **(B)** Coral rubble (Evhoe 2012), **(C)** Colonial scleractinians on hard substrate (Evhoe 2011), **(D)** Solitary scleractinians on hard substrate (BobEco 2011), **(E)** Antipatharians or gorgonians on hard substrate (Evhoe 2012), **(F)** Mixed corals on hard substrate (Evhoe 2009), **(G)** Colonial scleractinians on soft substrate (Evhoe 2012), **(H)** Solitary scleractinians on soft substrate (Evhoe 2011), **(I)** gorgonians on soft substrate (BobGeo 2009) and **(J)** Seapens on soft substrate (Evhoe 2010). Mixed corals on soft substrate is formed by the same species as **(I,J)**; therefore, a representative image of this habitat is not added. Copyright of all images in this figure: Ifremer. Ifremer provided permission for reproduction.

TABLE 3 | Information of the different coral habitats in the Bay of Biscay including the linear (with and without BobEco cruise, which had a sampling bias toward scleractinian corals); the environmental factors (mean and standard deviation σ); the abundances, densities, species richness, and diversity indices without *Madrepora oculata* (Mo), *Lophelia pertusa* (Lp), and *Solenosmilia variabilis* (Sv); the presence of these scleractinians, and the percent cover of substrate types.

Habitat	Linear (km)	Linear (km)—no bias	No. of canyons	Mean depth (m)	Mean temperature ($^{\circ}$ C)	Mean sigma-theta (kg/m ³)	Number of analyzed images	Number subset images	Number of segments	Median linear segment (m)	Abundances (no MoLpSv)	Density (ind. per image)	Richness (no MoLpSv)	ES ₁₆	Presence of MoLpSv	Mean % soft substrate	Mean % hard substrate	Mean % scleractinian coverage	Mean % live framework
Coral reef	10.8	3.7	10	852 (σ = 134)	11.1 (σ = 0.4)	27.27 (σ = 0.07)	982	611	106	65.3	3,208	5.3	32	5.50	Mo Lp	24.5 (σ = 22.8)	0.5 (σ = 5.0)	74.4 (σ = 23.5)	2.6 (σ = 2.6)
Coral rubble	18.1	3.4	21	828 (σ = 233)	10.8 (σ = 0.7)	27.32 (σ = 0.11)	1,240	883	162	54.5	672	0.8	26	7.23	Mo Lp	38.7 (σ = 29.9)	2.4 (σ = 9.5)	58.8 (σ = 30.2)	0.3 (σ = 0.9)
Colonial scleractinians HS	3.4	1.7	12	1,105 (σ = 234)	10.7 (σ = 0.4)	27.33 (σ = 0.07)	452	185	49	37.3	199	1.1	27	9.44	Mo Lp Sv	16.0 (σ = 26.3)	51.7 (σ = 37.5)	19.0 (σ = 25.1)	2.0 (σ = 4.2)
Solitary scleractinians HS	0.006	0.006	1	1,572	11.1	27.26	3	0	1	6.0	NA	NA	NA	NA	NA	NA	NA	NA	NA
Antipatharians/gorgonians HS	0.8	0.54	9	1,238 (σ = 487)	10.2 (σ = 1.2)	27.38 (σ = 0.13)	96	30	24	25.5	205	6.8	21	9.04	Mo Lp	33.6 (σ = 34.8)	65.0 (σ = 35.8)	1.4 (σ = 5.5)	0
Mixed corals HS	2.2	2.1	12	1,095 (σ = 251)	11.0 (σ = 0.5)	27.28 (σ = 0.08)	318	92	43	27.6	718	7.8	30	9.07	Mo Lp Sv	36.2 (σ = 34.6)	58.4 (σ = 34.3)	5.4 (σ = 12.7)	0.3 (σ = 1.1)
Colonial scleractinians SS	4.2	1.2	11	932 (σ = 125)	10.9 (σ = 0.5)	27.29 (σ = 0.09)	438	236	68	36.3	249	1.1	19	7.16	Mo Lp	59.4 (σ = 29.7)	3.0 (σ = 12.4)	36.8 (σ = 28.2)	1.5 (σ = 1.8)
Solitary scleractinians SS	0.47	0.39	5	826 (σ = 92)	10.8 (σ = 0.2)	27.32 (σ = 0.04)	35	21	6	62.4	75	3.6	4	2.96	—	100.0 (σ = 0.0)	0	0	0
Gorgonians SS	1.1	1.1	5	1,120 (σ = 346)	10.7 (σ = 0.6)	27.37 (σ = 0.11)	54	24	14	43.2	68	2.8	4	2.40	—	100.0 (σ = 0.0)	0	0	0
Seapens SS	6.7	5.2	8	901 (σ = 405)	10.9 (σ = 1.0)	27.27 (σ = 0.14)	553	257	54	64.3	877	3.4	12	2.72	Mo Lp	99.9 (σ = 0.4)	0	0.1 (σ = 0.4)	0
Mixed corals SS	0.37	0.37	3	1,040 (σ = 323)	10.8 (σ = 0.4)	27.36 (σ = 0.08)	20	11	5	37.8	16	1.5	2	2.00	—	100.0 (σ = 0.0)	0	0	0

The diversity indices are based on 16 individuals, the lowest number of individuals observed for one habitat. The mean coverage in percentages (%) of soft, hard, and biogenic (colonial scleractinians) substrate are also given, as well as the percentage of live scleractinian cover from the total image that is visible. The standard deviation σ is also given.

TABLE 4 | The abundances of the coral morpho-types within coral habitats of the Bay of Biscay.

Coral order	Coral morpho-type	Coral reef	Coral rubble	Colonial scleractinians HS	Antipatharians/ gorgonians	Mixed HS corals	Colonial scleractinians SS	Solitary scleractinians SS	Gorgonians SS	Seapens SS	Mixed corals SS	Total abundances	Min. depth (m)	Max. depth (m)
Alcyonacea (soft corals; suborder Alcyoniina)	<i>Alcyonacea</i> sp. 11		1									1	706	
	<i>Alcyoniina</i> sp. 1		1									1	872	
	<i>Alcyoniina</i> spp.	1					1					2	837	1,061
	<i>Nephtheidae</i> sp. 2	1		1		5						7	723	1,381
	<i>Nephtheidae</i> spp.	2	1	1		2						6	763	1,257
Alcyonacea (gorgonians; suborders Calcaxonia and Holaxonia)	<i>Acanella arbuscula</i>	6	4	4	27	14	13		60	2	9	139	704	2,039
	<i>Acanthogorgia</i> spp.	34	9	7		2	8					60	655	1,275
	<i>Chrysogorgia</i> sp. 1					1						1	1,257	
	<i>Gorgonian</i> sp. 11			2								2	1,734	
	<i>Gorgonian</i> sp. 14	2										2	814	
	<i>Gorgonian</i> sp. 15			3								3	1,734	
	<i>Gorgonian</i> sp. 16			2								2	1,652	
	<i>Gorgonian</i> sp. 17	1										1	908	
	<i>Gorgonian</i> sp. 18	1										1	856	
	<i>Gorgonian</i> sp. 19	1		1								2	793	953
	<i>Gorgonian</i> sp. 21			1								1	1,194	
	<i>Gorgonian</i> sp. 22	2	1									3	1,023	1,112
	<i>Gorgonian</i> spp.	3	12	13	1	9	3					41	694	2,029
	<i>Isididae</i> sp. 3				4							4	1,042	1,230
	<i>Keratoisis</i> sp. 3					1						1	1,257	
	<i>Lepidisis</i> sp. 2				27	11						38	1,233	1,995
	<i>Lepidisis</i> spp.					1						1	1,401	
	<i>Narella bellissima/N. regularis</i>	8	24	1		7	3					43	694	942
	<i>Narella versluysi</i>	238	214	39	1	70	115					677	678	1,734
	<i>Plexauridae</i> sp. 1	1	1		8							10	692	2,345
	<i>Plexauridae</i> spp.	1		1	18							20	779	1,867
	<i>Swiftia</i> sp. 1	3		2								5	805	956
Antipatharia	<i>Antipatharia</i> spp.	212	65	9	3	46	17			2		354	643	1,820
	<i>Antipathes</i> spp.	45	5		10	7	1					68	580	904
	<i>Antipathes dichotoma</i>	115	58		3	62	12					250	649	936
	<i>Antipathes viminalis</i>	29	1			9	1					40	658	1,285
	<i>Bathypathes</i> sp. 1	1				2						3	823	917

(Continued)

TABLE 4 | Continued

Coral order	Coral morpho-type	Coral reef	Coral rubble	Colonial scleractinians HS	Antipatharians/ gorgonians HS	Mixed corals HS	Colonial scleractinians SS	Solitary scleractinians SS	Gorgonians SS	Seapens SS	Mixed corals SS	Total abundances	Min. depth (m)	Max. depth (m)
	<i>Bathypathes</i> sp. 2	1	1	2	3	1						8	744	1,789
	<i>Bathypathes</i> sp. 3					1						1	1,051	
	<i>Chrysopathes</i> sp. 1		1									1	861	
	<i>Leiopathes</i> spp.	1,923	132	3		21	10					2,089	649	1,378
	<i>Parantipathes</i> sp. 1	83	55	7	4	70	16		1	2		238	656	1,583
	<i>Parantipathes</i> sp. 2	3		1		1	1					6	755	914
	<i>Stichopathes gravieri</i>	293	6	6	10	124	15					454	580	1,408
	<i>Trissopathes</i> spp.	33	4	9		9	3					58	763	1,275
Non-identified Anthozoa	<i>Anthozoa</i> sp. 7	6	15	8	7	101						137	717	1,408
	<i>Anthozoa</i> sp. 11		1	2	4	9						16	949	1,371
	<i>Anthozoa</i> sp. 13									2		2	855	900
	<i>Anthozoa</i> spp.	53	22	27	13	73	21	4		10		223	236	2,018
Pennatulacea	<i>Anthoptilum</i> sp. 1									1		1	797	
	<i>Distichoptilum gracile</i>									270		270	1,768	2,305
	<i>Funiculina quadrangularis</i>									11		11	236	253
	<i>Kophobelemnnon</i> cf. <i>stelliferum</i>							4	5	565	7	581	379	1,793
	<i>Pennatula</i> spp.									8		8	1,038	1,153
	<i>Pennatulacea</i> sp. 3								2	3		5	796	1,502
	<i>Pennatulacea</i> spp.				1					1		2	1,118	1,995
Scleractinia	<i>Caryophyllia</i> sp. 2	16				5	3					24	666	1,408
	<i>Caryophylliidae</i> sp. 7				13			5				18	657	1,085
	<i>Dendrophyllia cornigera</i>			3								3	556	
	<i>Desmophyllum</i> sp. 1	4	4									8	678	866
	<i>Enallopsammia rostrata</i>			22		7						29	1,106	1,408

(Continued)

TABLE 4 | Continued

Coral order	Coral morpho-type	Coral reef	Coral rubble	Colonial scleractinians HS	Colonial scleractinians HS	Colonial scleractinians SS	Solitary scleractinians SS	Gorgonians SS	Seapens SS	Mixed corals SS	Total abundances	Min. depth (m)	Max. depth (m)
	<i>Flabellidae</i> sp. 1		1			2	62				79	699	1,026
	<i>Solitary coral</i> spp.	86	33	22		4	34				183	476	1,995
	<i>Vaughanella</i> sp. 1					43					43	1,224	1,230
	<i>Madrepora oculata</i> and/or <i>Lophelia pertusa</i>	+	+	+		+			+			649	1,432
	<i>Solenosmilia variabilis</i>			+								1,228	1,819
Total		3,208	672	199	205	718	249	75	68	877	16	6,287	

The minimum and maximum water depths (m) for each morpho-type are given. If the species was observed only once (or several individuals on the same place), one depth value is given.

antipatharians (212 individuals). For the seapens SS habitat, *K. cf. stelliferum* and *Distichoptilum gracile* contributed to 95% of the total abundance.

In general, soft substrate habitats had a lower coral abundance, density and diversity than those of biogenic and hard substrate coral habitats. Exceptions are the coral abundance on seapens SS that is relatively high and the diversity on colonial scleractinians SS that is similar to that of biogenic habitats.

Community composition

Two PCAs were used to explore variations in coral community composition between habitats. In the co-variance PCA (Figure 4A), the relative abundances of the species are considered but for this reason, reef-forming corals were excluded. In the correlation PCA (Figure 4B), all species were included and characterized by either their abundances or percent cover, but data were normalized.

Without considering the reef-forming scleractinians, the coral composition discriminates hard substrate or biogenic habitats from soft substrate habitats along the first axis of the covariance PCA, explaining 42% of the variance. The only exception to this pattern is colonial scleractinian SS, which clusters with the hard substrate and biogenic habitats. This cluster of hard substrate, biogenic and colonial scleractinians SS habitats is dominated by the gorgonian *N. versluysi* as well as *Leiopathes* spp. and other unidentified antipatharians. The second axis of the PCA, explaining 18% of the variance in coral composition, discriminated the different soft substrate habitats, with gorgonian SS and mixed corals SS mainly dominated by the gorgonian *Acanella arbuscula*, seapens SS dominated by *K. cf. stelliferum* and *D. gracile* and solitary scleractinians SS dominated by a caryophyllid and a flabellid.

By adding the percent cover of colonial scleractinians in a correlation PCA, the coral composition further discriminates the habitats dominated by *L. pertusa*/*M. oculata* that form biogenic habitats (coral reef and coral rubble) and colonial scleractinians SS, from the habitats dominated by *S. variabilis* on hard substrate (colonial scleractinians HS). The former cluster of biogenic habitats is characterized by the occurrence of a mix of gorgonians and antipatharians while the later cluster of hard substrate habitats is colonized mainly by gorgonians. The only antipatharian (*Bathypathes* sp. 3), characterizing hard substrate habitats, was observed once. The morphotype Anthozoa sp. 7, either a gorgonian or an antipatharian, and a soft coral from the suborder Alcyoniina (*Nephtheidae* sp. 2) also characterizes hard substrate habitats. Solitary corals dominated biogenic reefs, on the other hand.

The abundances of antipatharians, gorgonians and seapens were significantly correlated with scleractinian coral cover (Figure 5). The abundance of antipatharians was positively correlated with each of the scleractinian cover measurements (live and dead framework, coral rubble, total framework and total coral cover), but most strongly with the total cover of framework ($r = 0.315$, $p \leq 0.001$). Of the three coral cover measurement separately, antipatharians correlated mostly with live coral framework ($r = 0.3$, $p \leq 0.001$) and the least with coral rubble ($r = 0.148$, $p \leq 0.001$). The abundance of gorgonians on

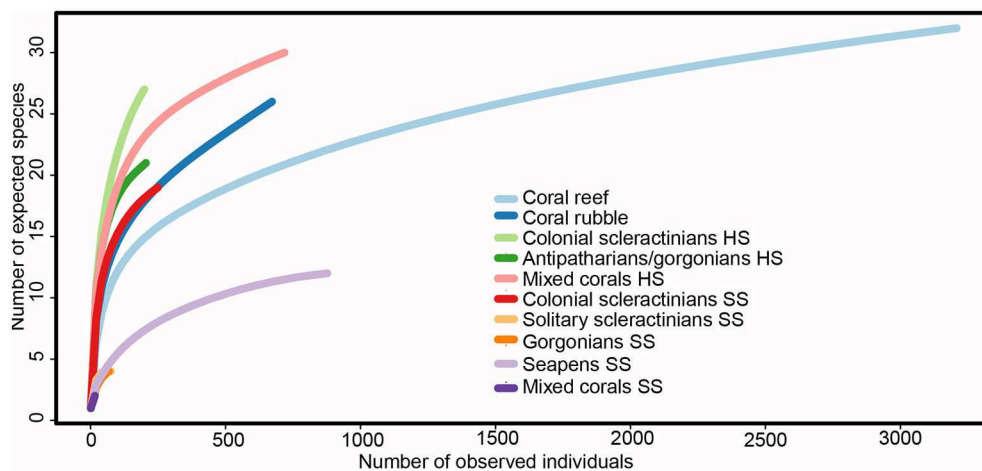


FIGURE 3 | Rarefaction curves of the coral habitats, excluding the reef-forming scleractinians *M. oculata*, *L. pertusa*, and *S. variabilis*. The number of species (y-axis) is based on the number of individuals (x-axis) in each habitat. Each color represents a different coral habitat.

hard substrate was also positively, but weakly, correlated with live and dead coral framework ($r = 0.162$, $p \leq 0.001$ and $r = 0.074$, $p \leq 0.001$, respectively). A significant correlation was found between the abundances of antipatharians and gorgonians on hard substrate ($r = 0.176$, $p \leq 0.001$).

The abundance of seapens were negatively correlated with each of the measurements of scleractinian coral cover as well as with antipatharians and gorgonians on hard substrate ($-0.123 \leq r \leq -0.414$; $p = 0.001$). The correlation of the abundance of gorgonians on soft substrate was negative with coral rubble and total cover ($r = -0.149$ and -0.156 , $p = 0.001$) but close to zero with the three different framework measures and antipatharian/gorgonian abundances.

Distribution of Coral Habitats

Coral habitats were observed in all 24 canyons of the Bay of Biscay that were surveyed during this study and on 39 out of 46 dives analyzed here (Tables 2, 5). On the upper slope between Odet and Blavet Canyons, no coral habitats were observed.

In most canyons, at least four different coral habitats were observed (55.6% of the canyons), up to a maximum of seven habitats in Lampaul and Odet Canyons (Figure 6, Tables 3, 5). Coral rubble was the most common (21 canyons) and mixed corals SS was the least common habitat observed (3 canyons). Reefs and colonial scleractinians on hard and soft substrate were always associated with coral rubble at the scale of individual canyons, except in Blackmud Canyon, where a small proportion of colonial scleractinians HS—scleractinians on a vertical wall—were observed (less than 0.1% of the total coral linear in this canyon), but no coral rubble. Coral rubble, on the other hand, was also observed in canyons where no live scleractinian habitats were encountered.

Overall, habitats formed by colonial scleractinians were absent in the southern part of the Bay of Biscay (Figure 6). One exception was the coral rubble habitat in Ars Canyon (linear =

173.7 m; 81.6% of the coral linear in that canyon). The Aquitaine margin was dominated by coral habitats on soft substrate (total linear = 2.1 km, corresponding to 90% of the coral habitat linear on this margin) (Figure 6).

A PCA was used to investigate (dis)similarities in habitat composition between canyons (Figure 7; Table 5). The first axis (explaining 31% of the variance) discriminates canyons dominated by hard substrate and/or biogenic habitats (including colonial scleractinians SS) from canyons dominated by soft sediment habitats. The three surveyed canyons incising the Aquitaine margin belonged to this second group. The second axis (explaining 19% of the variance) discriminates canyons dominated by habitats formed by *L. pertusa*/*M. oculata* from canyons dominated by other coral species on hard substrate. The PCA thus showed that the associations of coral habitats tend to characterize three groups of canyons: (i) canyons dominated by soft substrate habitats formed by other corals than reef-forming scleractinians, (ii) canyons dominated by reef, rubble and colonial scleractinians on soft substrate, and (iii) canyons dominated by hard substrate habitats.

Oceanographic and Geomorphological Settings

The coral habitats were observed mostly between 600 and 1,200 m water depth (Figure 8A; Table 3). Coral rubble was the shallowest (228 m; Odet-Guilvinec) and antipatharians/gorgonians HS the deepest (2,348 m; Athos) coral habitat. Seapens SS had the widest depth range of over 2,000 m (234–2,305 m water depth), while the narrowest depth range was 332 m (solitary scleractinians SS: from 752 to 1,085 m water depth).

Temperatures ranged from 7 to 12°C, with a mean temperature of 10.8°C (Figure 8B) and sigma-theta ranged from 27.11 to 27.64 kg/m³ (Figure 8C). Patterns of variations in temperature and water density between habitats were similar to the depth patterns.

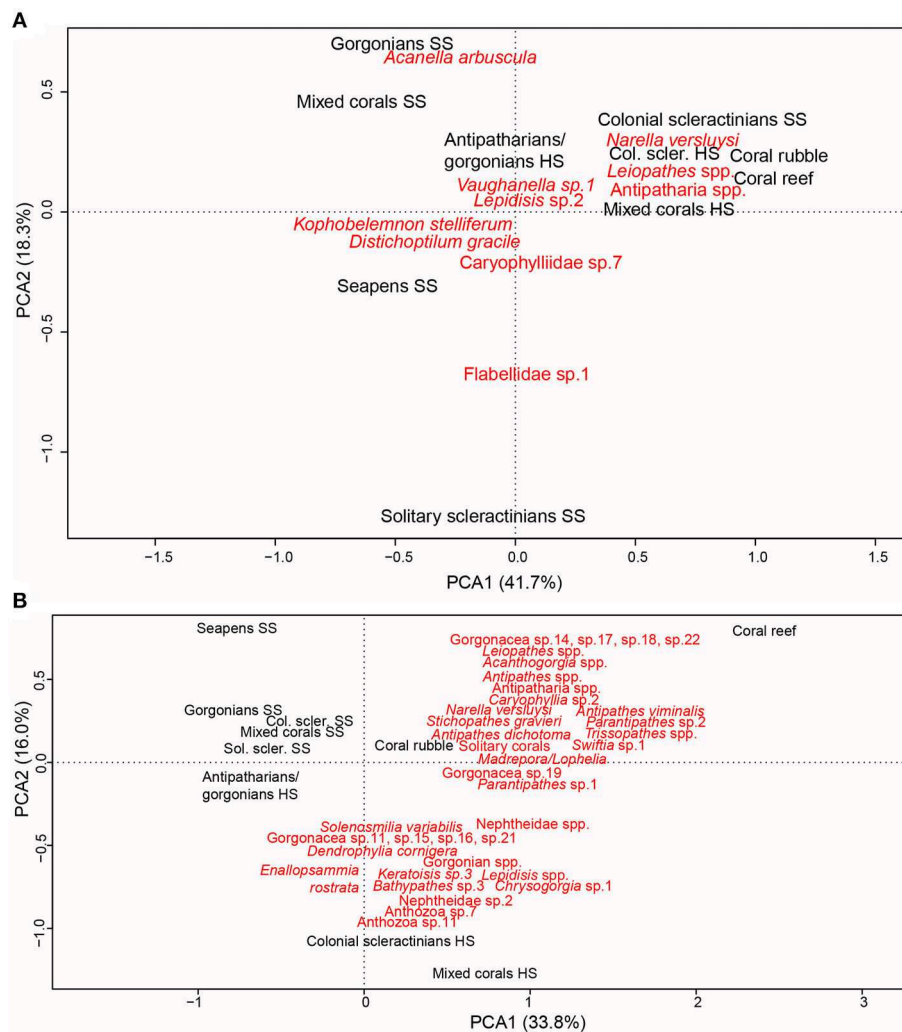


FIGURE 4 | Biplot ordination of the coral habitats (in black) and coral taxa (in red) in the two first axis of (A) a covariance PCA computed on Hellinger-transformed abundances of non-reef forming coral taxa per habitat. For clarity only those species contributing to at least 5% of the variance along one axis are represented. (B) A correlation PCA computed on raw abundances of non-reef forming corals or percent cover of reef-forming corals (*M. oculata*, *L. pertusa*, and *S. variabilis*). For clarity, only those species contributing for at least 3% of the variance along one axis are represented. Col. scler. SS, Colonial scleractinians SS; Sol. scler. SS, Solitary scleractinians SS.

BCAs investigated the relationship between coral habitats and habitat type and the oceanographic characteristics as well as the derivatives of the bathymetry to assess if these environmental setting vary among habitats (Table 5). Environmental multivariates were significantly different between habitats and habitat type ($p = 0.001$). The coral habitats, however, explained only 9.1% of the variance in environmental settings. Habitat type (hard substrate, soft substrate and biogenic substrate that included colonial scleractinians SS in this analysis) explained even less (5.3%).

The influence of geomorphology was assessed at a macro-scale by comparing the habitat distribution with the expert-supervised classification of geomorphological features. Coral habitats were observed on 12 of 15 classes on the 100 m resolution, while on

the higher (15/25 m) resolution these habitats were observed on 18 of 20 geomorphological classes (Supplementary Data S2). At both resolutions, the majority of images of coral habitats were located on canyon or interflue flanks, compared to other geomorphological classes.

The occurrences of coral habitats on the broadest scale of morphology—canyon, interflues and upper-slope—differed from a random distribution on both resolutions (high res.: $\chi^2 = 1,076$, $df = 18$, $p < 0.001$, Figure 9A; low res.: $\chi^2 = 289.2$, $df = 18$, $p < 0.001$). At both resolutions, and for most coral habitats, occurrences were more frequent in the canyons than on the interflues and the upper slope. The only consistent exception was coral rubble that was more frequent on the interflues/upper slope than in the canyons. The seapens SS habitat was also more

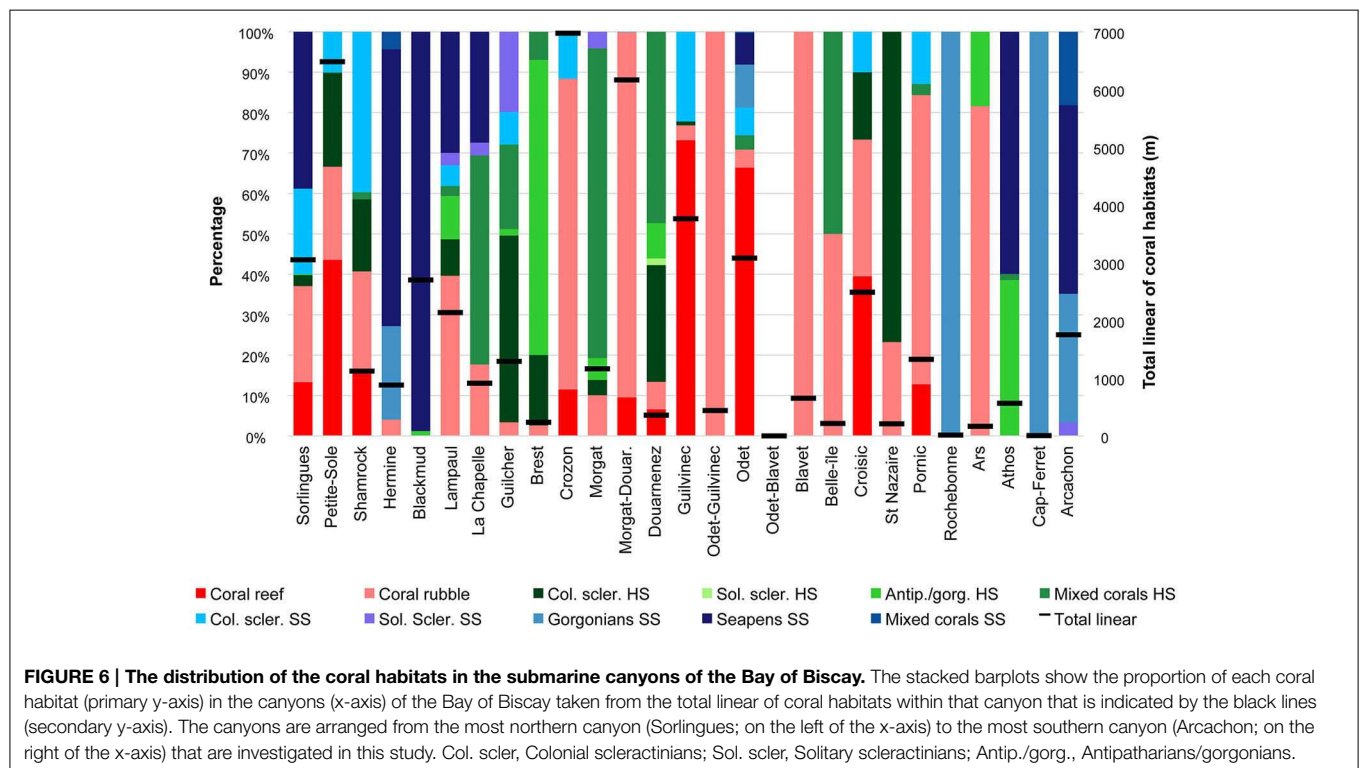
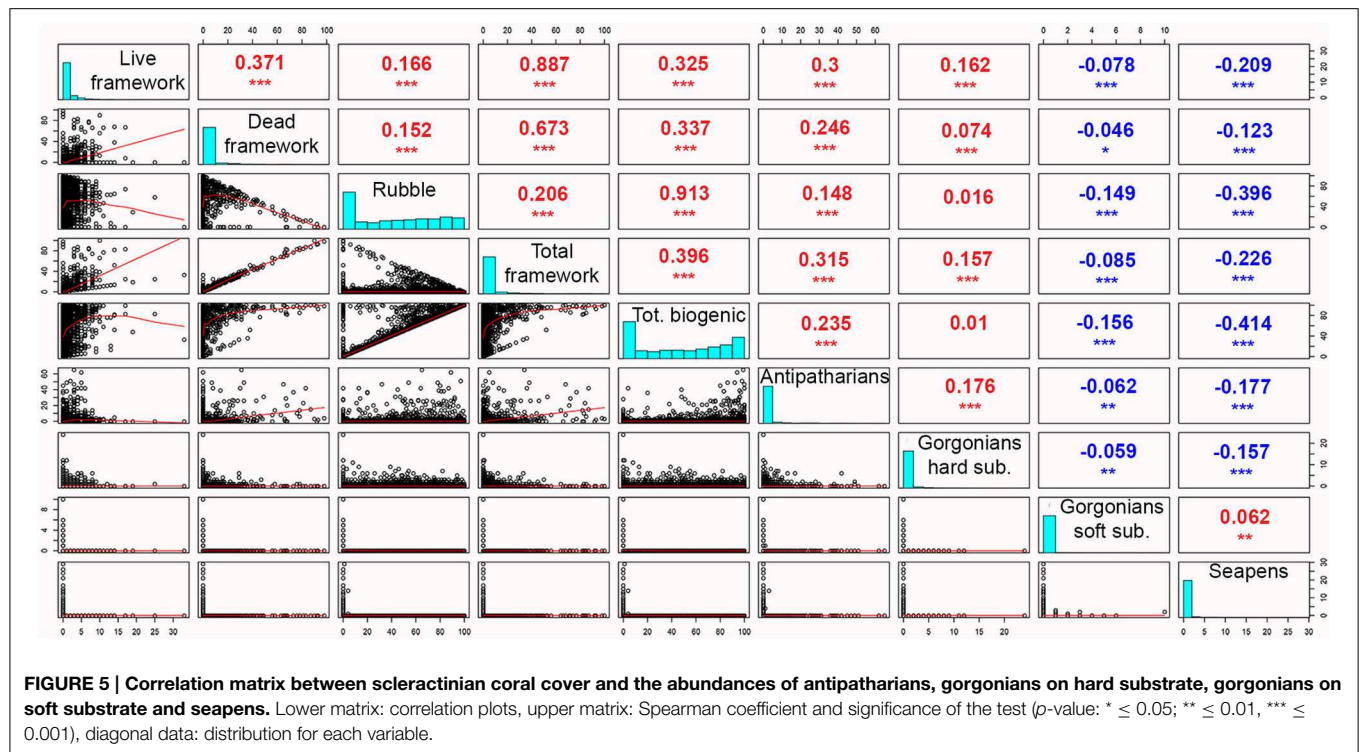


TABLE 5 | A description of the canyons including the linear of observed area, the percentage of coral habitat taken from the observed area linear (both biased and non-biased for scleractinians), the environmental settings of the canyons and the mean substrate cover (in percentages; standard deviation σ between brackets).

Canyons	Total linear (km)	Total linear observed area (km)	% Total coral habitats (all dives)	Total linear observed area (km) – non-biased dives	% Total coral habitats (non-biased dives)	Mean depth of survey area	Mean temperature of survey area	Mean salinity of survey area	Number of “subset” images	Number of coral habitats	Mean % soft substrate	Mean % scleractinian framework	Mean % hard substrate
Sorlingues	17.1	15.4	19.8	3.5	7.7	825.5	10.3	35.6	156	6	64.0 ($\sigma = 37.1$)	32.2 ($\sigma = 35.9$)	3.8 ($\sigma = 16.6$)
Petite-Sole	14.3	13.5	47.9	3.4	76.0	832.4	10.9	35.6	383	5	28.2 ($\sigma = 27.6$)	53.5 ($\sigma = 33.6$)	10.2 ($\sigma = 24.2$)
Shamrock	9.8	9.4	11.9	No bias	No bias	574.3	11.6	35.6	29	5	24.3 ($\sigma = 31.1$)	67.0 ($\sigma = 33.5$)	8.6 ($\sigma = 21.6$)
Hermine	5.7	5.7	15.5	No bias	No bias	1,046.7	10.6	35.7	24	4	99.0 ($\sigma = 3.2$)	1.0 ($\sigma = 3.2$)	0.0 ($\sigma = 0.0$)
Blackmud	5.3	5.2	51.9	No bias	No bias	888.9	11.3	35.6	83	3	99.4 ($\sigma = 5.7$)	0.0 ($\sigma = 0.0$)	0.6 ($\sigma = 5.7$)
Lampaul	21.3	18.5	11.5	0.0	–	1,363.3	9.8	35.6	167	7	69.4 ($\sigma = 36.1$)	15.1 ($\sigma = 22.4$)	15.5 ($\sigma = 32.7$)
La Chapelle	6.6	6.5	14.0	No bias	No bias	594.5	11.5	35.6	43	4	60.2 ($\sigma = 40.0$)	14.9 ($\sigma = 33.2$)	24.9 ($\sigma = 34.8$)
Guilcher	4.8	4.8	27.1	No bias	No bias	1,057.6	10.6	35.7	38	6	46.9 ($\sigma = 47.6$)	12.1 ($\sigma = 16.9$)	41.0 ($\sigma = 41.3$)
Brest	4.1	3.6	6.7	No bias	No bias	1,050.2	10.6	35.7	6	4	39.2 ($\sigma = 44.4$)	8.7 ($\sigma = 13.4$)	52.2 ($\sigma = 52.5$)
Crozon	10.3	9.3	75.1	0.0	–	961.1	10.0	35.6	361	3	43.3 ($\sigma = 26.2$)	55.8 ($\sigma = 26.8$)	0.8 ($\sigma = 3.0$)
Morgat	4.5	4.4	26.3	4.4	26.3	747.7	11.1	35.6	61	5	43.4 ($\sigma = 38.3$)	13.4 ($\sigma = 26.3$)	43.1 ($\sigma = 38.1$)
Morgat-Douarnenez	8.9	8.6	72.0	0.0	–	880.3	10.2	35.6	277	3	23.7 ($\sigma = 23.0$)	74.5 ($\sigma = 23.8$)	1.8 ($\sigma = 5.1$)
Douarnenez	4.0	4.0	9.0	No bias	No bias	1,091.3	11.3	35.6	14	6	30.2 ($\sigma = 36.3$)	4.8 ($\sigma = 10.8$)	65.0 ($\sigma = 39.9$)
Guilvinec	4.9	4.1	90.7	0.0	–	875.8	11.2	35.7	271	4	32.6 ($\sigma = 28.8$)	65.0 ($\sigma = 30.1$)	2.3 ($\sigma = 13.7$)
Odet-Guilvinec	0.7	0.7	59.1	No bias	No bias	228.7	11.8	35.7	13	1	25.5 ($\sigma = 31.8$)	74.5 ($\sigma = 31.8$)	0.0 ($\sigma = 0.0$)
Odet	14.3	14.2	21.7	No bias	No bias	700.2	11.4	35.7	135	7	45.8 ($\sigma = 36.4$)	52.1 ($\sigma = 37.1$)	2.1 ($\sigma = 12.7$)
Odet-Blavet	2.6	2.6	0.0	No bias	No bias	340.0	11.5	35.7	–	0	–	–	–
Blavet	5.8	5.8	11.4	No bias	No bias	324.7	12.0	35.7	18	1	25.2 ($\sigma = 28.1$)	74.8 ($\sigma = 28.2$)	0.1 ($\sigma = 0.2$)

(Continued)

TABLE 5 | Continued

Canyons	Total linear (km)	Total linear observed area (km)	% Total coral habitats (all dives)	Total linear observed area (km) – non-biased dives	% Total coral habitats (non-biased dives)	Mean depth of survey area	Mean temperature of survey area	Mean salinity of survey area	Number of “subset” images	Number of coral habitats	Mean % soft substrate	Mean % scleractinian framework	Mean % hard substrate
Belle-île	2.1	2.0	10.8	No bias	No bias	694.3	11.9	35.7	8	2	55.4 ($\sigma = 43.8$)	4.2 ($\sigma = 5.2$)	40.5 ($\sigma = 46.5$)
Croisic	4.1	3.9	63.4	0.0	–	852.0	11.2	35.7	159	4	26.9 ($\sigma = 28.0$)	53.3 ($\sigma = 35.3$)	19.8 ($\sigma = 33.4$)
St. Nazaire	2.6	1.9	10.9	0.0	–	1,552.8	11.1	35.7	9	2	6.1 ($\sigma = 18.4$)	24.2 ($\sigma = 23.9$)	69.7 ($\sigma = 24.0$)
Pornic	3.3	3.2	40.9	3.2	40.9	974.1	11.5	35.7	29	4	56.8 ($\sigma = 31.2$)	38.1 ($\sigma = 30.5$)	5.0 ($\sigma = 19.7$)
Rochebonne	3.6	1.6	1.0	0.0	–	1,022.8	10.5	35.7	1	1	100.0 (–)	0.0 (–)	0.0 (–)
Ars	6.6	5.7	3.0	3.6	3.8	781.0	11.3	35.7	9	2	22.8 ($\sigma = 24.0$)	61.4 ($\sigma = 42.1$)	15.8 ($\sigma = 31.4$)
Athos	10.3	9.8	5.8	No bias	No bias	1,508.0	9.3	35.5	10	3	94.4 ($\sigma = 12.5$)	0.0 ($\sigma = 0.0$)	5.6 ($\sigma = 12.5$)
Cap-Ferret	7.5	7.3	0.1	No bias	No bias	1,174.9	10.9	35.7	0	1	-	-	-
Arcachon	7.7	7.6	22.9	No bias	No bias	1,146.3	10.5	35.8	46	4	100.0 ($\sigma = 0.0$)	0.0 ($\sigma = 0.0$)	0.0 ($\sigma = 0.0$)
Bay of Biscay	192.5	179.5	26.8	107.3	18.3	968.4	10.8	35.6	2,350	11	43.2 ($\sigma = 35.9$)	46.9 ($\sigma = 36.5$)	8.5 ($\sigma = 23.6$)

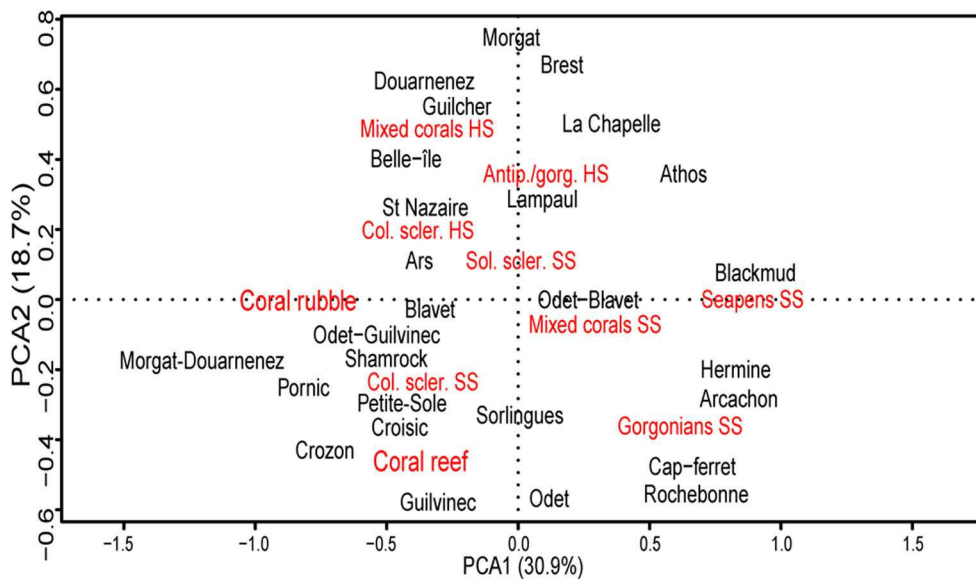


FIGURE 7 | Biplot ordination of canyons (in black) and coral habitats (in red) in the first two axis of a covariance PCA computed on the Hellinger-transformed linear of coral habitats per canyon. The Solitary scleractinians HS habitat was removed prior to analysis. Antip./gorg., Antipatharians/gorgonians; Col. scler., Colonial scleractinians; Sol. scler., Solitary scleractinians.

frequent on the interflues according to the low bathymetric resolution but this pattern was not consistent at the high resolution (data not shown). The location on the northwestern or southeastern flanks of canyons and interflues also had a significant influence on the occurrences of coral habitats (high res.: $\chi^2 = 511.89$, $df = 10$, $p < 0.001$, **Figure 9B**; low res.: $\chi^2 = 598.71$, $df = 9$, $p < 0.001$). At both resolutions, the occurrences of most coral habitats were more frequent on the northwestern flank than on the southeastern flank. The seapens SS and mixed corals HS habitats were coherent exceptions, with more occurrences on the southeastern flank. Finally, the influence of slope on the coral habitats was also investigated. At both high and low resolution, slope had a significant influence on the distribution of coral habitats (high res.: $\chi^2 = 595.84$, $df = 27$, $p < 0.001$, **Figure 9C**; low res.: $\chi^2 = 1,140.9$, $df = 27$, $p < 0.001$). The slope, however, mainly influenced hard substrate and biogenic habitats while its influence was low on soft substrate habitats. Furthermore, the distribution of coral rubble was highly skewed toward smoother slopes compared to all other habitats. These two patterns were consistent at both resolutions. The colonial scleractinians HS and seapens SS habitats were also more frequently observed on smoother slopes ($<10^\circ$), but on only one of the bathymetrical resolutions, respectively the low or high resolution (data not shown).

DISCUSSION

This study greatly increases the knowledge of coral habitats in the Bay of Biscay including a large number of canyons and a high diversity of coral habitats representing a total linear of nearly 50 km. Thus far, there have been few studies within the Bay of

Biscay. They mainly focused on scleractinian species (Joubin, 1922; Zibrowius, 1980; Reveillaud et al., 2008) and facies (Le Danois, 1948; De Mol et al., 2011; Sanchez et al., 2014) or coral habitats and assemblages, in Whittard, Dangeard or Explorer Canyons (Howell et al., 2011; Huvenne et al., 2011; Morris et al., 2013; Davies et al., 2014; Robert et al., 2015).

Le Danois (1948) described both scleractinian and sand/mud facies on the continental margin of the Bay of Biscay as one of the first studies in this basin. He observed (i) aggregations of the seapens *K. stelliferum*, *Umbellula* spp., and *Pennatula* spp. emerging from muddy bottoms between 500 and 1,000 m depth, particularly in the north and south of the basin, (ii) scleractinian facies formed by the reef-forming species *L. pertusa*, *M. oculata*, and *S. variabilis* on the Celtic and Armorican margins, and (iii) several gorgonians, antipatharians and solitary scleractinians that were associated with this scleractinian facies including some species that are also observed in the present study, e.g., *N. versluysi* and *Antipathes dichotoma*. The present study included canyons that were not visited by Le Danois (1948) and habitats were seen *in situ* on the image footage. However, it was not possible to precisely compare distribution patterns with the present study because of low positioning accuracy (before GPS) in Le Danois (1948)'s study.

Influence of Substrate Type

Distribution of Coral Habitats at Regional and Canyon Scales

The distribution of CWC habitats is heterogeneous in the canyons of the Bay of Biscay. The majority of canyons in this study hosts four or more and up to seven, coral habitats in the same canyon. The heterogeneity in the distribution of coral

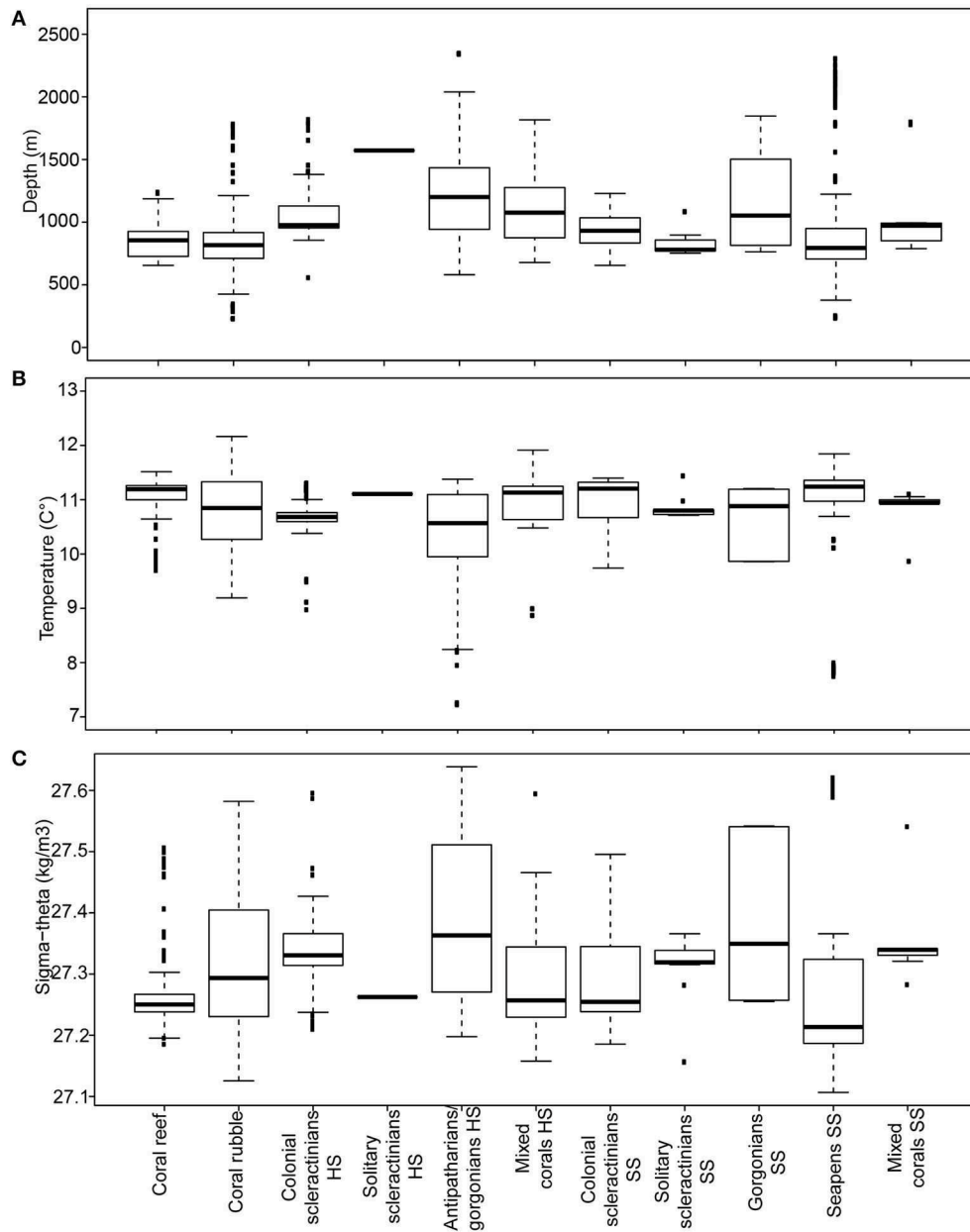


FIGURE 8 | Boxplots of (A) depth, (B) temperature, (C) water density (sigma-theta) for the 11 coral habitats observed in the Bay of Biscay.

habitats seems to be largely driven by the substratum type, both at the scale of the Bay of Biscay and at the scale of canyons; the most important patterns being (i) the absence of live scleractinian habitats in canyons on the southern Armorican margin and the Aquitaine margin and (ii) the dominance of habitats on soft substrate in canyons incising the Aquitaine margin.

At the canyon scale, canyons can be divided into three groups based on their dominant substrate type, depending on their coral habitat composition. The canyon grouping matches with the mean percentage of substrate cover within each group (soft, hard, and/or scleractinians).

In general, the canyons in the southern part of the Bay of Biscay are smoother and more sedimentary without geomorphological features known for their hard substrate when compared with canyons in the northern or central parts of the Bay of Biscay which present falls and cliffs (Bourillet et al., 2010). The canyons on the Aquitaine margin also seem to have a different sedimentation regime, because of their shorter distance to the shore (Mulder et al., 2012; Schmidt et al., 2014), similar to Nazaré Canyon (de Stigter et al., 2007). The southern canyons, e.g., Cap-Ferret and Capbreton Canyons exhibit higher sedimentation rates and more recent sediment input than

canyons on the Armorican margin (Mulder et al., 2012; Schmidt et al., 2014). This sediment was not being remobilized due to the low internal wave energy and lower current speeds in the canyons of the Aquitaine margin (Koutsikopoulos and Le Cann, 1996; Mulder et al., 2012), preventing erosion and, therefore, the exposure of hard substrate. This erosion is observed in Blackmud, Audierne and Guilvinec Canyons on the northern and central Armorican margin (Mulder et al., 2012; Khrpounoff et al., 2014). Such a regime of higher sedimentation toward the southern Bay of Biscay likely explains both the quasi absence of scleractinian habitats and the dominance of soft substrate habitats on the southern Armorican margin and the Aquitaine margin.

Variations in sedimentation regime at canyon scale may also account for some of the variability in habitat composition and explain the statistically significant differences observed in the distribution of scleractinian and seapen habitats between the flanks of canyons. The Blackmud Canyon provides a good example. Due to its location on the Armorican margin, elevated currents and lack of recent sedimentation (Mulder et al., 2012), this canyon was a good candidate for scleractinian habitats. However, only the southeastern flank could have been explored, which turned out to be dominated by seapens on soft substrate.

This asymmetry in canyons—one eroded flank and one sedimentary flank—has been previously observed in the Bay of Biscay (Van Rooij et al., 2010; De Mol et al., 2011; Huvenne et al., 2011; Sanchez et al., 2014), in the Mediterranean (Orejas et al., 2009; Fabri et al., 2014) and off Canada (Mortensen and Buhl-Mortensen, 2005). The observed asymmetry is due to a dominated current, e.g., a westerly current in Cassidaigne Canyon, or dense shelf water cascading in Cap de Creus and Lacaze-Duthiers Canyons (Orejas et al., 2009; Fabri et al., 2014). In the Bay of Biscay, the slope current flows polewards along the slope (Pingree and Le Cann, 1989, 1992; Koutsikopoulos and Le Cann, 1996) in a dominant southeastern—northwestern direction, eroding the northwestern flank from canyons and exposing hard substrate on this flank. This important current in the Bay of Biscay has therefore been suggested to favor the development of species needing hard substratum on the northwestern flank compared to the more sedimentary southeastern flank (Van Rooij et al., 2010). In the present study, however, the occurrence of mixed corals on hard substrate on the sedimentary southeastern flank contradicts previous observations and hypothesis. This habitat occurred more often on steep areas with slopes of more than 20°, suggesting that this apparent exception may be due to the steep topography itself or the accelerated currents it forms preventing deposition of sediment. This local prevention of sediment deposition may potentially lead to the occasional exposure of hard substrate on the southeastern flank of canyons.

To summarize, the distribution patterns of coral habitats—a dominance of soft substrate habitats in canyons of the Aquitaine margin and an absence of live scleractinian habitats in the southern Bay of Biscay—can be related to the substrate heterogeneity, influenced by differences in morphology and hydrology, at the scale of the Bay of Biscay. Coral habitat distribution also varies at a canyon scale, due to an asymmetry of hydrological regimes within canyons, leading

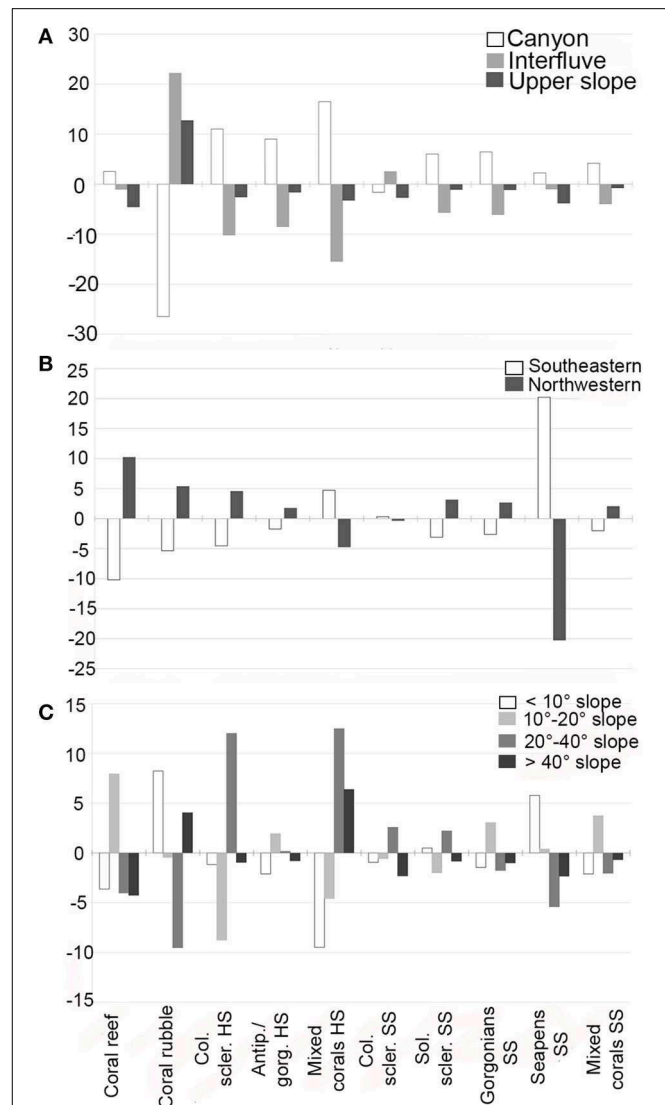


FIGURE 9 | Standard residuals of chi-square tests of the frequency of images of each habitat on (A) the different canyon morphologies, (B) the southeastern and northwestern flank of the canyon/interflaves, and (C) the four slope intervals of the canyon/interflaves flank. If the residuals are less than -2 , the observed frequency is less than the expected frequency according to a random distribution. If the residual is greater than 2 , the observed frequency is greater than the expected frequency. The lower (< -2) or higher (> 2) the residual value is, the stronger is the contribution of this category to the observed distribution. Col. scler. HS, Colonial scleractinians HS; Antip./Gorg. HS, Antipatharians/gorgonians HS; Col. scler. SS, Colonial scleractinians SS; Sol. Scler. SS, Solitary scleractinians SS.

to eroded northwestern flanks that enhance the colonization by scleractinians and more sedimentary southeastern flanks favoring soft sediment habitats.

Variability of Coral Assemblages among Substrate Type

Coral habitats in the Bay of Biscay are dominated by the three reef-forming scleractinians as well as the antipatharian *Leiopathes*

spp., the gorgonian *N. versluysi* and the seapen *K. cf. stelliferum*. Coral assemblages, however, are much more diverse than these few dominant species. A total of 62 coral morphotypes were identified in this study. The composition of coral assemblages and the correlations between coral densities or cover all indicated a clear dichotomy between soft sediment dominated habitats and hard substrate/biogenic habitats.

Corals are usually specialized in either hard or soft substrate. Seapens are adapted to live in soft sediment by a peduncle which anchors the colony in the sediment (Williams, 1995). Most antipatharians, colonial scleractinians and most gorgonians need hard substrate to settle (Roberts et al., 2009; Wagner et al., 2012). Members of the gorgonian family Isididae, e.g., *A. arbuscula*, can also occur in soft sediment due to a root-like holdfast (e.g., Mortensen and Buhl-Mortensen, 2005; Wienberg et al., 2009).

The biogenic and hard substrate habitats share coral morphotypes and clustered together in the PCA excluding the three reef-forming scleractinians. The coral assemblage of colonial scleractinians on soft substrate habitat also clustered with these habitats, despite the dominance of soft sediment in this habitat. Coral species preferring hard substrate could settle on the scleractinian framework emerging from the soft sediment. These corals, therefore, can be present in a habitat with a non-optimal substrate cover, as was observed in Nora Canyon in the Mediterranean Sea (Taviani et al., in press). With the addition of the reef-forming scleractinians in the analysis, the biogenic reef assemblages differed from those on hard substratum; in reef, *L. pertusa*/*M. oculata* colonies are present, while *S. variabilis* is absent. Additionally, the reef composition is characterized by different gorgonian morphotypes than that of hard substrate habitats and it also includes antipatharians and solitary corals, that are almost absent in hard substrate habitats.

While the biogenic and hard substrate habitats shared some species, the coral assemblages of the soft substrate habitats (excluding colonial scleractinians) differ more from each other as shown by the PCA (Figure 4A), and thus, show a higher species turnover. The alpha-diversity of these habitats is also generally lower than that of the coral assemblages of biogenic and hard substrate habitats. The mixed corals on soft substrate habitat is characterized by the gorgonian *A. arbuscula*, also characterizing gorgonians on soft substrate, but it also includes the seapen *K. cf. stelliferum*, characterizing the seapens habitat. The few segments of this mixed coral habitat are surrounded by either gorgonian or seapen habitat, what could suggest that the mixed coral habitat may function as a “transition” zone between the gorgonian or seapen habitats. Even though these three habitats share *K. cf. stelliferum* and *A. arbuscula*, the PCA does separate the seapen habitat from the other two soft sediment habitats, due to other seapen species, e.g., *D. gracile*, which were exclusively seen in the seapens habitat.

Influence of Internal Tides and Geomorphology on Coral Habitats

Hydrodynamics, such as downwelling and tidal currents, that may be influenced by the local seafloor topography, are important for the food transport and supply to CWCs, as shown in the

Mingulay Reef Complex (Davies et al., 2009) and Rockall Bank (Soetaert et al., 2016). The Bay of Biscay is characterized by peculiar hydrodynamics mainly due to the numerous canyons and the steep continental slope. Tidal currents strengthened along the canyon seafloor and internal waves on the upper part of the slope favor exchanges between deep and superficial water masses and are reported in several canyons in this basin (Pingree and Mardell, 1985; de Madron et al., 1999; Mulder et al., 2012; Pichon et al., 2013; Khripounoff et al., 2014). Measurements from Guilvinec canyon, for example, show internal waves with vertical speeds enhancing the renewal of water with considerable daily variations in temperature, salinity and oxygen (Khripounoff et al., 2014). Thus, it increases the amount of suspended material, a potential food for CWCs, that could move to water depths up to 2,800 m (Pichon et al., 2013), corresponding to the observed maximum water depth of antipatharians/gorgonians on hard substrate habitat in this study. Coral habitats can also be related to benthic nepheloid layers, as observed in Cap-Ferret Canyon (de Madron et al., 1999) including a layer at the same depth (1,850 m) as gorgonians on soft substrate habitat.

The presence of coral habitats in this study indicates that corals are able to form habitats (with a minimum size of 25 m² according to the CoralFISH definition) on hard or soft bottoms within the canyons of the Bay of Biscay, but the environmental factors available at the resolution in this study did not discriminate habitats. Several habitat suitability models have predicted that the canyons are indeed (highly) suitable for octocorals (Yesson et al., 2012), antipatharians (Yesson et al., in press) and colonial scleractinians (Davies and Guinotte, 2011), but temperature, salinity, water density, slope, rugosity and bathymetric position index (BPI) came out as important factors in these models controlling the distribution (Davies and Guinotte, 2011; Howell et al., 2011; Yesson et al., 2012, in press; Robert et al., 2015). Most “habitat” suitability models were, however, devoted to predict occurrences of the coral (sub)order or species only and the results may not be the same if the suitability of habitats is being predicted (Howell et al., 2011), similarly to the model of Robert et al. (2015) predicting abundances, species richness and diversity.

Nevertheless, with an estimated height between 10 and 60 cm emerging from the sediment of which the majority is dead, scleractinian reefs in the Bay of Biscay appear to be lower than those described in other areas along the NE Atlantic margins; scleractinian reefs along the coast of Norway are very high, between 2 and 33 m, and the outermost part is dominated by live *L. pertusa* colonies (Mortensen et al., 2001; Flogel et al., 2014) and carbonate mounds off Ireland, built up by dead scleractinian framework and sediment, can also reach up to several hundreds of meters high, covered by coral rubble on the flanks and live *L. pertusa* and/or *M. oculata* colonies (~0.75–1 m in height) on the summit (Huvenne et al., 2005, 2007; Wheeler et al., 2005, 2007). The area covered by the reefs in the Bay of Biscay also appears smaller. The minimum size of an individual Norwegian reef is ~50 m in diameter, while the largest measures ~500 m (Mortensen et al., 2001). The live

scleractinian reef covering the summits of carbonate mounds off Ireland can approach 500 m in size (Huvenne et al., 2005). Approximately three quarters of the reef segments in our study are smaller than 100 m in linear and almost 15% is smaller than 25 m (26% if all coral habitats are considered). Therefore, although CWCs find suitable conditions to form habitats on hard or soft bottom in the canyons of the Bay of Biscay, scleractinian corals do not inhabit their optimal conditions here, as observed in northern continental margins of the NE Atlantic. This may be due to high sedimentation rates (that may be too high for prestige scleractinian reefs) in canyons, a potential difference in hydrology, the steepness of the topography and/or differences in food supply and quality. Nevertheless, the diversity of CWC habitats and species identify the Bay of Biscay as an essential section or transition zone for coral habitats between the north European margin and the Mediterranean, as it is suggested by Reveillaud et al. (2008) and De Mol et al. (2011).

There is a high overlap between the predicted suitable areas of these coral orders/species, including the canyons for all corals (Davies and Guinotte, 2011; Yesson et al., 2012, in press). This pattern is emphasized by the present study as the environmental factors (e.g., temperature), as well as the derivatives of the 100 m resolution bathymetry do not discriminate a specific environment for each coral habitat. In other words, CWC habitats in the Bay of Biscay share similar environmental settings, at the resolution at which these environmental factors are available. The size of coral habitats, of which most segments measured less than 100 m, compared to the resolution of the environmental factors, ranging from 100 m to 0.083° latitude (~10 km) easily explain the difficulty to discriminate particular environmental settings for the different coral habitats. The observed pattern also points out the limits of habitat suitability models which were based on a rather low resolution of oceanographic parameters (0.04°–1° latitude) (Davies et al., 2008; Davies and Guinotte, 2011; Yesson et al., 2012). Limited resolution understandably causes uncertainties in habitat mapping and suitability models (Davies and Guinotte, 2011; Rengstorf et al., 2012) whereby some local features, such as individual coral habitats, could be missed. The bathymetry is often available in high(er) resolutions for a mosaic of better studied areas associated with specific cruises. A comparison of models using different resolutions of bathymetrical data resulted into significant changes in the predictive habitat suitability maps, and a minimum resolution of 250 m was determined as necessary to identify individual coral mounds (Rengstorf et al., 2012). In our study, the slope classes (of the geomorphological classes with a 15/25 m resolution) resulted in differential coral habitat distribution; live coral habitats tend to occur on steeper areas (>10°) and coral rubble on flatter areas (<10°), an influence that appeared to be stronger for hard substrate and biogenic habitats than for soft substrate habitats.

These results suggest the importance of high resolution environmental datasets that allow to study the link between environment and habitat. Habitat maps with high resolution data, thus predicting specific habitat distributions, could feed into marine spatial planning plans.

Advantages and Limitations of a Habitat Classification System

The use of a classification system is useful for habitat mapping and therefore interesting for conservation initiatives such as OSPAR (Oslo-Paris Convention) and ICES (the International Council for the Exploration of the Sea). A classification system permits the use of a standardized habitat description over large areas. The CoralFISH classification system was developed to deliver standardized terminology across the CoralFISH regions, especially for marine management purposes (Davies et al., in press). It encompasses both species and their environment, a scale suggested to be most accurate and ecological relevant for spatial planning and conservation (Costello, 2009). Using a classification system to analyze images is less time-consuming (at least four times) than a detailed analysis to the species level. Besides, the risk of misidentification is lower at a habitat level than at species level. However, a classification system also has limitations. Firstly, the diversity associated with habitats, i.e., here 62 morphotypes, is masked by the use of only the structuring species. Second, a classification system can skew conservation efforts by assigning a higher weight to similar habitats. For example, in the present case, five hard substrate/biogenic habitats and one soft substrate habitat with similar compositions could be considered as one management unit, whereas the four soft substrate habitats with different species compositions should be considered as four different units. Third, several international organizations favor their preservation of certain habitats, including corals and sponges, but have different definitions of a habitat that cannot be all captured in one classification. The CoralFISH classification is close to the classification of FAO Vulnerable Marine Ecosystems (ICES) but is difficult to adapt to the definitions of “reefs” used by the EC Habitats Directive that considers all hard substrate, whether colonized or not (European Commission, 2013). Fourth, the habitats are *a priori* assumptions or hypotheses about the association of biology and physiography and therefore cannot be analyzed *a posteriori* to test the reliability of these hypotheses, i.e., the link between biology and geology. And finally, the habitat scale focuses on an aggregation of structuring individuals on a certain surface unit, but exclude the isolated occurrences or aggregations smaller than this unit, thus, it does not reflect the realized distribution of coral species.

Classification systems are, therefore, useful for conservation because they provide information about habitat distribution rapidly compared to analyses at the species level, yet they limit the ability to understand the biology and ecology of species.

Conservation

Threats and Canyons as Refuges for CWC Habitats

The submarine canyons in the Bay of Biscay host a large range of coral habitats, making them an important target for marine management and conservation. Coral habitats are threatened by human activities of which litter and fisheries are the main impacts in the Bay of Biscay.

Litter, including lost fishing gear, is largely present in the canyons of the Bay of Biscay (Galgani et al., 1995; van den Beld et al., in press). Corals, boulders and other features forming relief

on the seafloor are important structures that can trap litter (e.g., Galgani et al., 2000) as shown by the presence of more litter items in areas with a seafloor relief formed by geological or biological features than without a relief (Watters et al., 2010; Bergmann and Klages, 2012; Schlining et al., 2013; van den Beld et al., in press).

Bottom trawling is probably one of the largest anthropogenic threats to CWCs (Fosså et al., 2002; Hall-Spencer et al., 2002; Benn et al., 2010) and this fishing activity is increasing on the rims of canyons (Martín et al., 2014b). Trawl gear can damage CWC communities by reducing or changing coral abundances, diversity and community or the removal of structuring species (reviewed by Clark et al., 2016), as shown for coral reefs of the NE Atlantic (Hall-Spencer et al., 2002) and *Solenosmilia* thickets on Australian seamounts (Althaus et al., 2009). In addition to damages caused by physical contact with trawl gear, trawling can have an indirect impact on CWCs. It causes extensive sediment resuspension in the water column that is transported further down the canyon and it changes the seafloor relief by smoothening canyon flanks through repeatedly scraping off the seafloor resulting in homogeneous slopes and low rugosity (Puig et al., 2012; Martín et al., 2014a). These effects can also have an impact on CWCs and associated community.

Canyons are less accessible for trawling gears than the interflues and upper slope due to their steep and complex topography and, therefore, may function as a natural refuge for CWCs (Huvenne et al., 2011; Fernandez-Arcaya et al., 2017). The results of this present study support this hypothesis. Most (live) habitats, including coral reef, occurred more frequently in the canyons than on the interflues or upper slope. A consistent exception was coral rubble that was more frequent on the interflues and upper slope than in the canyon. Furthermore, live coral habitats are more frequently observed on steeper areas, hardly accessible to trawling, while coral rubble is more often observed on flatter areas. Similarly to the last result, the highest number of corals in Whittard Canyon has been observed on areas with steep slopes (Morris et al., 2013).

Impact by fisheries may have an influence on the fields of rubble on shallow areas, such as the upper slope, and the presence of live corals in canyons. Previous evidence from the 1920s show that fishermen trawling around and on the continental slope of the Bay of Biscay, had caught *L. pertusa* and *M. oculata* in their nets (Joubin, 1922).

Natural causes also influence the distribution of coral species and habitats. Live corals, such as scleractinians, may prefer steep topography over flatter areas, which could be related to for example accelerated currents. Furthermore, environmental changes over time, such as sea temperature elevation since the Last Glacial Maximum, can cause the death and breakdown of CWCs. In Guilvinec and Penmarc'h Canyons, age measurements suggested that the dead scleractinian corals, occurring in shallower waters (200–300 m), are older (~7–8 ka) than the live corals deeper (600–700 m) in the canyon (~1–2 ka) (De Mol et al., 2011). The authors suggested that both trawling and natural events could cause these dead corals.

Besides coral rubble, the seapen habitat is also observed in shallow waters (from 234 m water depth), on areas with a slope value less than 20° and is more common on interflues

than in the canyon (100 m res.). Some seapen species can retract completely within the sediment, as has been observed for *Protoptilum carpenteri* (Packer et al., 2007; Baker et al., 2012) and *K. stelliferum*, *Pennatula phosphorea*, and *Virgularia mirabilis* (De Clippele et al., 2015). This may suggest that some seapen species are resilient to trawling compared to other corals. It may be also possible that seapens (re)colonize an area more rapidly than colonial scleractinians. However, it may also be possible that trawling does not take place as shallow as certain seapens, as it is suggested for *Funiculina quadrangularis* (not able to withdraw in the sediment) occurring at 240 m water depth in Mediterranean canyons (Fabri et al., 2014).

In summary, our results support the hypothesis that canyons may function as natural refuges for coral habitats. Trawling may cause the observed distribution of live habitats favoring steep slopes, but the influence of natural causes cannot be excluded. Seapens exhibit specific features that may make them more resilient to trawling and may explain their similar distribution to coral rubble, compared to other coral habitats.

Conservation in the French Bay of Biscay

Submarine canyons are “hotspots” for coral habitats and could serve as natural refuges for certain coral habitats. However, conservation measures are rare in the Bay of Biscay. Until the present day, there are two measures on the Aquitaine margin. A fishing restricted area is in place around Capbreton Canyon since 1985, prohibiting certain types of fishing around this canyon (Sanchez et al., 2013). Under the EC Birds Directive, a Special Protection Area (SPA) has been designated at the head of Cap-Ferret Canyon, but does not include management measures of relevance for benthic habitats.

This study fed into a proposal to define sectors for a network of Natura 2000 sites to protect reef habitats under the Habitats Directive (MNHN-SPN and GIS-Posidonie, 2014). The designation of a Natura 2000 network comprising submarine canyons is a step forward in the protection of deep-sea habitats in the French Atlantic.

The Natura 2000 management measures will, however, not apply to soft sediment coral habitats, because this type of habitat does not fall under the Habitats Directives. Although the diversity was low, the (possible) unique species compositions may make them potential candidates for protection. The OSPAR commission does have “Seapen and burrowing megafauna communities” and “Coral gardens” listed as threatened and/or declining habitats (OSPAR, 2008) recognizing its potential vulnerability to anthropogenic impact, but most of the seapen communities remain unprotected by any form of legislation. Seapens can have an important value for humans, supported by the presence of burrows made by e.g., the commercially important crustacean *Nephrops norvegicus* (langoustine) (OSPAR, 2010) and associations of fish larvae, e.g., *Sebastes* spp., with seapens (Baillon et al., 2012).

CONCLUSIONS

This study included 24 canyons and the results reported here, thus, largely increases the understanding of the distribution of

CWC habitats in submarine canyons of the Bay of Biscay. A general regional pattern can be suggested, with a dominance of soft substrate coral habitats and an absence of live scleractinian habitats in the south. Results support the importance of the substrate type on the habitat distribution at different spatial scales, with coral assemblages mostly differentiated in hard/biogenic vs. soft substrate coral communities. The latter one harbors a lower coral diversity and distinct coral compositions between habitats. The overlap of environmental conditions associated with distinct coral habitats can be due to the resolution of the habitats and environmental factors. However, it may also be possible that some discriminating differences exist that would be caused by features that could not be included in this study, e.g., current speed and exposition to current. The geomorphological classes may also provide a good indication of the kind of environment favoring coral habitat development, if data are available with a high enough resolution. Provided this link would be better understood, such classes would help inform management plans, with a less detailed and time-consuming image collection and analysis required than a species level analysis. This study may also open doors for potential management for soft substrate coral habitats, each of which appeared to be structured by a different morphotype.

AUTHOR CONTRIBUTIONS

Collection of the biological data: IV, BG, JD, SA, and JB. Design of image analysis protocol: IV, JD, BG, and LM. Image analysis: IV. Statistical analysis: IV and LM. Collection/analysis/interpretation of bathymetry and geomorphological classes: JB and LC. Wrote the paper: IV, LM, and KO. Critically reviewed the paper: JB, SA, LC, JD, and BG. Chief-scientists of cruises: SA and JB.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <http://journal.frontiersin.org/article/10.3389/fmars.2017.00118/full#supplementary-material>

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Chapter 4

The diversity of species associated with coral habitats in submarine canyons of the Bay of Biscay

Résumé français

La diversité des espèces associées aux habitats coralliens dans les canyons sous-marins du Golfe de Gascogne

1. Introduction

Les récifs de coraux d'eau froide, construits par les scléactiniaires *Lophelia pertusa* et *Madrepora oculata*, sont considérés comme des *hotspots* de biodiversité et de biomasse benthique (par ex. Roberts *et al.*, 2006 ; Van Oevelen *et al.*, 2009 ; Freiwald *et al.*, 2004). Ils fourniraient des fonctions pour d'autres organismes, comme des refuges, des zones d'alimentation et des nurseries (par ex. Freiwald *et al.*, 2004 ; Roberts *et al.*, 2006). Les scléactiniaires forment une structure tridimensionnelle qui crée une hétérogénéité d'habitat. Cette hétérogénéité pourrait favoriser la densité et la diversité de la faune associée. Les agrégations formées par des coraux d'eau froide non-récifaux, comme les gorgones, antipathaires et pennatules, pourraient avoir des fonctions similaires aux récifs car les colonies de coraux créent un relief sur le fond marin, donc une hétérogénéité d'habitat (Tissot *et al.*, 2006).

Ces habitats coralliens sont particulièrement sensibles aux perturbations physiques, en particulier le chalutage (Clark *et al.*, 2016 ; Ramirez-Llodra *et al.*, 2011). La préservation de leur structure et leurs fonctions nécessitent des mesures de gestion adaptées.

Les habitats coralliens trouvent dans les canyons sous-marins un environnement favorable à leur développement, grâce à des régimes hydrologiques et sédimentaires particuliers ainsi qu'une topographie complexe et accidentée (par ex. De Leo *et al.*, 2010 ; Mortensen et Buhl-Mortensen, 2005). La marge continentale française du Golfe de Gascogne est incisée par de nombreux canyons sous-marins (Bourillet *et al.*, 2006). Dans ces canyons, des récifs de coraux construits par *L. pertusa* et *M. oculata*, des zones de débris de scléactiniaires et des jardins de pennatules ont été observés (De Mol *et al.*, 2011 ; Le Danois, 1948). Plus récemment, d'autres habitats coralliens ont été observés dans ces canyons (Van den Beld *et al.*, soumis), mais la faune associée aux habitats coralliens est peu connue.

Dans cette étude, la communauté d'espèces associée aux habitats coralliens dans les canyons sous-marins du Golfe de Gascogne a été examinée. Les habitats coralliens ont été définis *a priori* (Van den Beld *et al.*, soumis) suivant la classification des habitats coralliens produite par le projet CoralFISH (Davies *et al.*, 2017). Cette classification définit les habitats en fonction de l'espèce dominante et du type de substrat (Davies *et al.*, 2017). Dix habitats coralliens sont observés dans les canyons du Golfe de Gascogne (Van den Beld *et al.*, 2017). L'influence du substrat, liée à des processus hydrodynamiques et de sédimentation, est très important et divise les habitats en trois catégories : (i) les habitats biogéniques, incluant les récifs, les débris de coraux et les colonies isolées de scléactiniaires sur substrat meuble, (ii) les habitats dominés par le substrat dur, structurés par des scléactiniaires coloniaux, des antipathaires et des gorgones, et (iii) les habitats dominés par le substrat meuble, structurés par des scléactiniaires solitaires, des gorgones (*Acanella arbuscula*) et des pennatules (Van den Beld *et al.*, 2017).

Les objectifs de cette étude étaient de tester si la classification des habitats coralliens *a priori* se traduirait par des différences de densité, de diversité et de composition des espèces associées. L'hypothèse est que les habitats biogéniques auraient une diversité et une densité plus élevées que d'autres habitats coralliens compte tenu de leur structure tridimensionnelle et complexe ainsi que l'hétérogénéité des substrats. En outre, une deuxième hypothèse formulée est que, dans les habitats biogéniques, la diversité et la densité de la faune associée seraient positivement corrélées avec la couverture de substrat biogénique.

2. Matériels et méthodes

Quarante-six plongées ont été réalisées pendant sept campagnes océanographiques entre 2009 et 2012 (BobGeo, BobGeo 2, BobEco, Evhoe 2009, 2010, 2011, 2012) (Table 1). Pendant ces campagnes, 24 canyons et trois sites sur les interfluves ou le haut de pente contigu à deux canyons ont été visités par un *Remotely Operated Vehicle* (ROV) ou une caméra tractée.

Chaque image acquise a subi un contrôle qualité (éclairage, netteté, distance au fond) avant d'être annoté. Pour toutes les images exploitables, l'habitat a été défini suivant la classification du projet CoralFISH (Davies *et al.*, 2017).

Un sous-ensemble des images a été sélectionné avec un pas temps d'une minute depuis le début de la plongée. Sur ces images, la couverture de substrat a été évaluée en pourcentage et la mégafaune a été comptée et identifiée au niveau de résolution taxonomique le plus élevé permis par l'image. La résolution taxonomique varie du phylum à l'espèce. Chaque taxon identifié est défini comme un morphotype. Pour chaque spécimen, le type de substrat sur lequel il est fixé ou associé a été annoté. Des espèces de poisson pouvaient être associées à des structures géologiques, par exemple une roche, ou biologiques, par exemple un antipathaire ou une éponge.

Le comportement trophique de chaque morphotype a été défini d'après la littérature (Bowden *et al.* (2016), Rowden *et al.* (2010), Fauchald et Jumars (1979), Shepard *et al.* (1986), Whitehead *et al.* (1984 ; 1986a ; 1986b) et le « World Register of Marine Species » (WORMS; www.marinespecies.org).

Afin de tester l'influence du substrat, les habitats coralliens ont été groupés en trois grandes classes : les habitats biogéniques (récifs, débris de coraux et les scléactiniaires coloniaux sur substrat meuble), les habitats coralliens sur substrat dur (scléactiniaires coloniaux, antipathaires/gorgones et des coraux mixtes sur substrat dur), et les habitats coralliens sur substrat meuble (scléactiniaires solitaires, gorgones, pennatules et des coraux mixtes sur substrat meuble).

3. Résultats

Au total, 32.589 individus ont été observés dont 31.127 ou 95,6% sont associés à un morphotype. Un total de 191 taxa a été identifié dont 160 à une résolution taxonomique qui permet de les assimiler à des morphotypes uniques. Les analyses de diversité portent uniquement sur ces 160 morphotypes.

Les densités de la faune associée étaient différentes entre les habitats coralliens (Kruskal Wallis: $\chi^2 = 118153$, $df = 9$, $p < 0.0001$) (Fig. 1A). En particulier, les densités étaient élevées sur les habitats de coraux mixtes sur substrat dur et les récifs de coraux. En fonction du substrat (Fig. 1B), la densité la plus élevée a été observée dans les habitats coralliens sur substrat dur ($50,8 \pm 86,9$; médiane = 10,6), suivi par les habitats biogéniques ($11,9 \pm 16,7$; médiane = 6,0). La densité la plus faible a été observée sur les habitats coralliens sur substrat meuble ($4,9 \pm 4,2$; médiane = 4,0). Les différences étaient significatives (Kruskal Wallis: $\chi^2 = 33.209$, $df = 2$, $p < 0.0001$; Fig 1B).

Les patrons de dominance étaient variables entre habitats coralliens (Fig. 3). Les brachiopodes dominaient les habitats coralliens sur substrat dur. Les échinodermes, en particulier le comatule *Koehlermetra porrecta*, et les cnidaires dominaient ou codominaient les habitats biogéniques. Les habitats coralliens sur substrat meuble se caractérisaient par l'absence d'une dominance marquée et donc une équitabilité élevée.

Les richesses spécifiques moyennes par image étaient différentes entre les habitats coralliens (Kruskal-Wallis: $\chi^2 = 48,911$, $df = 9$, $p < 0,01$) (Fig. 4A). La richesse spécifique était en particulier élevée sur les habitats de coraux mixtes sur substrat dur. En fonction du substrat, la richesse spécifique n'était pas significativement différente (Fig. 4B).

Les indices de Chao I et d'ES₂₈ d'Hurlbert, ont montré que, en général, la diversité de la faune associée aux habitats biogéniques était plus élevée que la diversité sur les habitats coralliens sur substrat dur (Table 2). La diversité de la faune associée aux habitats coralliens sur substrat meuble était similaire ou même plus élevée que la diversité sur les habitats biogéniques. Les courbes de raréfaction ont cependant également montré que ces habitats coralliens sur substrats meubles étaient sous-échantillonnés (Fig. 5).

L'analyse en composante principale de la composition des assemblages de mégafaune distinguaient trois groupes d'habitats coralliens : (i) les habitats biogéniques caractérisés par la comatule *K. porrecta*, (ii) les habitats coralliens sur substrat dur caractérisés par les brachiopodes, et (iii) les habitats coralliens sur substrat meuble caractérisés par de nombreux morphotypes, comme *Bolocera* sp. 1 et Cerianthidae sp. 1 (Fig. 6).

L'influence des taux de couverture ou de l'abondance des coraux d'eau froide sur la faune associée a été étudiée (Fig. 9). Les tests de corrélation de Spearman ont montré des corrélations significatives entre les taux de couverture ou densité de coraux et la densité de la faune associée, mais les coefficients de corrélation sont faibles (Fig. 9A). A l'échelle des habitats, cependant, la diversité des espèces associées (ES₂₈) était significativement et négativement corrélée à la diversité des espèces coralliennes (ES₁₆) (Fig. 9B).

Les individus associés aux habitats coralliens étaient principalement des filtreurs/suspensivores, à l'exception de l'habitat de scléactiniaires solitaires sur substrat meuble qui était dominé par des brouteurs (Fig. 10). En général, les proportions de filtreurs/suspensivores étaient plus faibles sur les habitats coralliens sur substrat meuble que celles sur les habitats biogéniques et sur les habitats coralliens sur substrat dur (Fig. 10). Les prédateurs, comme les crustacés et les poissons se trouvent dans tous les habitats.

Les comatules (échinodermes), surtout l'espèce *K. porrecta*, dominaient la faune associée aux matrices de scléactiniaires récifaux *L. pertusa* et *M. oculata* (et dans une moindre mesure *Solenosmilia variabilis*) (Fig. 11A et 11B) tandis que les zoanthaires (cnidaires) dominaient la faune fixée à des espèces de mégafaune autres que les scléactiniaires. D'autres groupes de cnidaires, les anémones et les cérianthes, dominaient les déchets marins et le substrat meuble, respectivement. Les brachiopodes enfin dominaient la faune fixée sur substrats durs et mixtes. La faune mobile observée à proximité d'une structure tridimensionnelle biologique était dominée par les poissons tandis que les structures géologiques attiraient autant les poissons et que les crustacés.

4. Discussion

Cette étude décrit la structure et la composition des communautés de mégafaune associées aux habitats coralliens des canyons sous-marins du Golfe de Gascogne. Les résultats principaux sont (i) les communautés se caractérisent par des diversités-beta et -gamma élevées, et (ii) la diversité-beta est particulièrement élevée entre les habitats biogéniques, de substrats durs et de substrats meubles.

Les habitats sur substrat dur sont caractérisés par une densité élevée et une diversité faible, dominés par une espèce de brachiopode. Les habitats biogéniques sont caractérisés par une densité intermédiaire et une diversité élevée, dominés par la comatule *K. porrecta*. Les habitats coralliens sur substrat meuble sont caractérisés par des densités faibles mais une diversité élevée.

Ces patrons de structure et de composition pourraient résulter de pressions de compétition et d'hétérogénéités environnementales différentielles entre les trois grands types d'habitat.

La compétition intra- et interspécifique pour des ressources, comme de l'espace et de la nourriture, influence la structure et la composition des communautés, mais est très peu étudiée en environnement profond (McClain et Schlacher, 2015). Généralement, la compétition entre espèces, surtout pour l'espace, est plus forte sur les habitats benthiques de substrat dur que sur les habitats de substrat meuble (Grant, 2000 ; Menge et Sutherland, 1976 ; Wilson, 1990). La relative équitabilité des morphotypes sur les habitats coralliens de substrat meuble comparée à la dominance de brachiopodes dans les habitats coralliens sur substrat dur et de la comatule *K. porrecta* sur les habitats biogéniques, est cohérente avec une pression de compétition plus faible sur les habitats de substrat meuble, ce qui pourrait contribuer à expliquer leur diversité locale plus forte.

La structure tri-dimensionnelle des matrices de coraux récifaux pourrait fournir de nombreuses micro-niches (Mortensen *et al.*, 1995 ; Roberts *et al.*, 2006) et par conséquent pourrait favoriser d'autres organismes (Roberts *et al.*, 2009). Nos résultats suggèrent que les récifs de coraux hébergent effectivement une communauté dense dans les canyons sous-marins du Golfe de Gascogne. La densité de la faune associée aux récifs de coraux était plus élevée que les densités de la faune associées aux autres habitats à scléactiniaires (débris de coraux et scléactiniaires coloniaux sur des substrats dur et meuble).

Les matrices de récifs pourraient fournir des ressources pour d'autres espèces. *K. porrecta* pourrait obtenir une position plus élevée dans la colonne d'eau lui permettant d'augmenter les probabilités d'attraper de la nourriture (Buhl-Mortensen *et al.*, 2010). Cette espèce était particulièrement abondante dans les récifs de *L. pertusa* et *M. oculata*. Les échinoïdes, par ex. *Cidaris cidaris*, ont également été observés sur cette matrice, où ils se nourrissent probablement de polypes de *L. pertusa* et *M. oculata*, du mucus sécrété par ces coraux ou d'autres petits organismes entre les branches (Rogers, 1999 ; Stevenson et Rocha, 2013 ; Vertino *et al.*, 2010 ; Wild *et al.*, 2008).

L'hétérogénéité de substrat des habitats biogéniques pourrait également influencer la diversité et la composition des communautés de faune associées (Buhl-Mortensen *et al.*, 2012 ; Davies *et al.*, 2014 ; Kenchington *et al.*, 2014). Les récifs dans les canyons sous-marins du Golfe de Gascogne ont une hétérogénéité de substrat élevée, créée par une alternance de substrat dur formé par de la matrice à scléactiniaires et de substrat meuble entre les colonies. Cette hétérogénéité pourrait expliquer les 71 morphotypes partagés entre les habitats biogéniques et d'autres habitats coralliens dominés par le substrat dur ou substrat meuble. En outre, la matrice à scléactiniaires pourrait servir comme refuge (Costello *et al.*, 2005 ; Mortensen *et al.*, 1995). Les observations de crustacé *Munida* sp. entre les branches de scléactiniaires récifaux viennent étayer cette hypothèse ; les *Munida* pourraient se cacher de leur principal prédateur, le poisson *Brosme brosme* (Kutti *et al.*, 2015).

5. Conclusion

Cette étude décrit les communautés de faune associées aux habitats coralliens dans les canyons sous-marins du Golfe de Gascogne. Conformément à notre hypothèse de départ, la faune associée aux habitats biogéniques dont les récifs coralliens est dense et diversifiée, mais contrairement à notre hypothèse de départ la diversité de la faune associée aux habitats coralliens sur substrat meuble, au moins l'habitat formé par des pennatules, semble au moins aussi élevée que celle des habitats biogéniques. Ces résultats demandent à être confirmés par un effort d'échantillonnage plus conséquent mais suggèrent que les habitats coralliens de substrat meuble ont un rôle fonctionnel important et devraient être pris en compte dans les stratégies de gestion de la biodiversité profonde.

Les patrons de communauté pourraient être déterminés la compétition intra et interspécifiques ou la différenciation de la niche. Les fortes dominances des comatules sur les habitats biogéniques et des brachiopodes sur les substrats durs contrastent avec l'équitabilité élevée au sein des habitats coralliens de substrat meuble. Ce patron suggère que la pression de compétition pourrait être plus faible sur les habitats de substrat meuble, ce qui contribuerait aux diversités élevées de cet habitat. La structure complexe et tri-dimensionnelle de la matrice à scléactiniaires, fournissant de multiples micro-niches, pourrait être importante pour augmenter la densité et diversité de la faune associée ; les deux mesures étaient plus élevées sur des récifs de coraux que les autres habitats formés par des scléactiniaires coloniaux avec une structure tri-dimensionnelle plus petite.

The diversity of species associated with coral habitats in submarine canyons of the Bay of Biscay

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Abstract

Cold-water coral (CWC) reefs constructed by the scleractinians *Lophelia pertusa* and *Madrepora oculata*, are considered as biodiversity and biomass hotspots, because of the functions they provide for other organisms, such as shelter and feeding grounds. The three-dimensional structure formed by the scleractinian framework can have an important role in enhancing this diversity. Aggregations of other CWCs, e.g. gorgonians and sea pens, may have similar functions as coral reefs in the deep sea. Biodiversity is an important factor feeding into many conservation plans aiming to protect CWC habitats that could be impacted by many human activities, especially bottom trawling.

CWC habitats occur in submarine canyons incising many continental margins, due to the specific heterogeneous hydrological and geological environment of submarine canyons. Since the late nineteenth century, CWCs are known to exist in the Bay of Biscay. Only a handful of studies investigated CWC habitats and their associated community in the canyons of this basin. While many of these studies focused on scleractinians, a high variety of CWCs habitats has been recently reported, which potentially increase the beta-diversity of associated faunal communities. This study investigated ten coral habitats in twenty-four canyons and three locations between adjacent canyons with an ROV or a towed camera to describe the diversity and composition of the megafaunal community associated with these coral habitats, and analyse the role of habitat as structuring factor of this biodiversity.

The composition of megafaunal assemblages was mainly driven by substrate type and clustered the habitats into three groups: (i) biogenic habitats, (ii) hard substrate habitats, and (iii) soft substrate habitats. The crinoid *Koehlermetra porrecta* was dominant on the biogenic habitats and brachiopods on the hard substrate CWC habitats, whereas no dominance patterns and a high species turn-over characterised soft substrate CWC habitats.

Diversity measurements varied between habitats but overall, the diversity of biogenic habitats was indeed high. Surprisingly, the diversity of the megafaunal community associated with soft bottom coral habitats appeared to be similar or even higher than biogenic or hard substrate CWC habitats, despite undersampling.

1. Introduction

Reefs formed by the colonial scleractinians *Lophelia pertusa* and *Madrepora oculata* are the most known and studied of cold-water coral habitats, especially in the North-East Atlantic Ocean (Roberts *et al.*, 2006). These *Lophelia* reefs are thought to have important functions to other organisms, including commercially important fish (e.g. Costello *et al.*, 2005; Jensen and Frederiksen, 1992). These three-dimensional habitats provide shelter for many species, and function as feeding grounds and nurseries for fishes (Costello *et al.*, 2005). *Lophelia* reefs are also considered as biodiversity and biomass hotspots (Jensen and Frederiksen, 1992; Roberts *et al.*, 2006; Van Oevelen *et al.*, 2009; Vetter *et al.*, 2010). The densities and diversity of these coral reefs exceeded the densities and diversity observed on the surrounding soft bottom communities or coral rubble areas for macrofaunal (Buhl-Mortensen *et al.*, 2012; Henry and Roberts, 2007; Mortensen and Fosså, 2006), megafaunal (Buhl-Mortensen *et al.*, 2012; Mortensen *et al.*, 1995) and fish communities (Costello *et al.*, 2005; Husebø *et al.*, 2002).

The heterogeneity created by the three-dimensional structure of scleractinian corals is thought to increase the biodiversity of the fauna associated with them, because it provides or enhances resources to other organisms, such as hard substratum and food (Buhl-Mortensen *et al.*, 2010; Mortensen *et al.*, 1995). Prey organisms could hide within the scleractinian framework and other organisms, especially filter-feeders, could benefit from the elevated structure of the coral framework to be higher in the water column and therefore in the benthic boundary layer that convey particulate organic matter (Buhl-Mortensen *et al.*, 2010; De Clippele *et al.*, 2015).

Besides reef-forming corals, aggregations of antipatharians, gorgonians and sea pens, may have similar functions as reefs (Freiwald *et al.*, 2004). Large aggregations of these cold-water corals, i.e. coral gardens, also provide shelter for prey and commensal filter-feeders benefit from a position higher up in the benthic boundary layer (Buhl-Mortensen *et al.*, 2010). Sea pen gardens could create habitat heterogeneity on sandy and muddy bottoms by structuring an area with low relief (Buhl-Mortensen *et al.*, 2010; Tissot *et al.*, 2006). In addition, larvae of redfish (*Sebastes* sp.) associating with seapens suggest that these CWCs may provide nurseries for fish (Baillon *et al.*, 2012). However, the community of coral habitats on soft sediments was usually estimated to be low in densities and diversity compared to rocky and biogenic habitats (Davies *et al.*, 2015; Robert *et al.*, 2015).

The high biodiversity that characterise CWC habitats, especially coral reefs, plays a key role in the conservation of cold-water coral according to multiple international organisations and directives, such as the UNGA (United Nations General Assembly: UNGA, 2006), the Convention of Biological Diversity (CBD, 2010), the EC Habitats Directive (Council Directive

92/43/EEC: EEC, 1992) and the EC Marine Strategy Framework Directive (Directive 2008/56/EC: EC, 2008). In addition, CWC habitats are threatened by many human activities, especially trawling (Clark *et al.*, 2016; Ramirez-Llodra *et al.*, 2011). They form therefore important conservation targets.

CWC habitats are known to exist in submarine canyons, due to a suitable hydrological regime coupled with the complex topography of canyons (De Leo *et al.*, 2010). The French continental margin of the Bay of Biscay is incised by more than 100 canyons (Bourillet *et al.*, 2006). Within these canyons, coral reefs and rubble fields constructed by *L. pertusa* and *M. oculata* as well as pennatulacean fields were observed (De Mol *et al.*, 2011; Le Danois, 1948). However, a recent study by Van den Beld *et al.* (2017) showed that, besides these habitats, other coral habitats also occur in this region. These habitats are constructed by a large variety of corals (antipatharians, colonial and solitary scleractinians, gorgonians and sea pens) that emerge from either hard substrate or soft sediment (Van den Beld *et al.*, 2017).

In the present study, the species community associated with coral habitats in submarine canyons of the Bay of Biscay were investigated. The habitats were defined *a priori* according to a classification of CWC habitats that considered both dominance patterns and substrate types (Davies *et al.*, 2017). Ten coral habitats, excluding one occurrence of an additional coral habitat, were observed in the Bay of Biscay which distribution patterns could be linked to the interplay of substrate type and hydrodynamics (Van den Beld *et al.*, 2017). Three types of coral habitats were distinguished by their coral assemblages: (i) biogenic habitats, including coral reef, coral rubble and colonial scleractinians on soft substrate, mainly constructed by the reef-building scleractinians *L. pertusa* and *M. oculata*, (ii) hard substrate CWC habitats constructed by colonial scleractinians, especially the reef-building coral *Solenosmilia variabilis* or by antipatharians, gorgonians or a mix of corals, and (iii) soft substrate CWC habitats constructed by solitary scleractinians, gorgonians (*Acanella arbuscula*) or pennatulaceans.

The objectives of this study were to test whether the *a priori* classification of CWC habitats translates into differences in the density, diversity and composition of the associated fauna. If differences are indeed observed, we further investigated whether CWC habitats could be ranked according the diversity and/or the density of their associated assemblages. We hypothesized that considering their three-dimensional complexity and substrate heterogeneity, biogenic habitats – habitats dominated by reef-building scleractinian framework or rubble – will show higher diversity and density than the other habitats. We further hypothesized that associated species diversity and density would be positively correlated with biogenic substrate cover and coral colony density.

2. Material and Methods

2.1. Study site

The continental slope of the Bay of Biscay, North-East Atlantic, is incised with numerous canyons and is divided from north to south into the Celtic, Armorican and Aquitaine margins (Bourillet *et al.*, 2006). A detailed description of the study site, including the hydrological regime, is given by Van den Beld *et al.* (2017).

The characteristics and distribution of coral habitats in the submarine canyons have been studied previously by Van den Beld *et al.* (2017). Almost 50 km of coral habitats were observed across the Bay of Biscay, divided into 531 segments. Ten coral habitats composed by colonial or solitary scleractinians, antipatharians, gorgonians and/or sea pens, dominated by biogenic (reef-building scleractinian framework or rubble), hard or soft substrate, were identified. *M. oculata*/*L. pertusa* reef and rubble were the most observed habitats, followed by sea pens on soft substrate.

The distribution was heterogeneous on multiple spatial scales: (1) soft sediment coral habitats dominated and live scleractinian habitats were absent in the southern region of the Bay of Biscay (Van den Beld *et al.*, 2017), where the canyons are smoother and more sedimentary than the canyons in the north and central Bay of Biscay (Bourillet *et al.*, 2010; De Chambure *et al.*, 2013), due to weaker hydrodynamics (Koutsikopoulos and Le Cann, 1996) and higher sedimentation rates (Mulder *et al.*, 2012; Schmidt *et al.*, 2014), and 2) the to the dominant current exposed northwestern canyon flank favoured scleractinians and the opposite southeastern flank favoured the soft sediment dominated sea pen habitat (Van den Beld *et al.*, 2017).

The structure and composition of coral species within the ten habitats have also been explored by Van den Beld *et al.* (2017). The main findings were: (1) the coral assemblages of the hard substrate dominated habitats and biogenic habitats shared certain species, but were separated by the colonial scleractinians *Solenosmilia variabilis* and *L. pertusa*/*M. oculata* respectively, (2) there was a higher coral species turnover on the soft sediment dominated coral habitats, that were mainly composed by only one coral species, and (3) the alpha-diversity of the soft substrate dominated coral habitats was usually lower than the biogenic or hard substrate dominated habitats. Substrate type was an important driver of the patterns in coral composition. Within the study to the non-coral associated fauna, the previous coral habitats have been merged into three categories, based on the dominant substrate type. The structure and composition of corals in the soft substrate dominated habitat ‘colonial scleractinians on soft substrate’ appeared to be similar to the biogenic habitats ‘coral reef’ and ‘coral rubble’ (Van den Beld *et al.*, 2017). Therefore, it was decided to consider this habitat as a biogenic habitat instead of a soft sediment dominated habitat within this study. The biogenic habitats are ‘coral reef’, ‘coral rubble’ and ‘colonial scleractinians on soft substrate’, the hard substrate dominated habitats are composed by ‘colonial scleractinians’, ‘antipatharians/gorgonians’ or ‘mixed corals’ and the soft sediment dominated habitats are composed by ‘solitary scleractinians’, ‘gorgonians’, ‘sea pens’ or ‘mixed corals’. Coral habitats are referred to as the structuring type of coral combined with an abbreviation of the substrate type, either HS for hard substrate or SS for soft substrate. For

example: antipatharians/gorgonians HS is a hard substrate dominated habitats structured by antipatharians or gorgonians. Reef and rubble are indicated as they are.

2.2. Optical surveys

Seven cruises on the R/V *Pourquoi Pas?*, on the R/V *Le Suroît* or on the R/V *Thalassa* between 2009 and 2012 were performed to collect data (Table 1).

Forty-three dives took place in 24 canyons (Table 1). Three additional dives were performed on the upper slope or interflaves between adjacent canyons; both canyon names were used to refer to these dives (Morgat-Douarnenez: dive BE480, Odet-Guilvinec: BG2_05, and Odet-Blavet: BG1_08; Table 1). Most canyons were already named prior to collection. The canyon just north of Éperon Ostrea, however, did not. The reference term ‘La Chapelle’ will be used in this paper, to simplify the reference to this particular canyon. The reference term is after an area of sand waves on the continental shelf near the head of this canyon that is called ‘haut-fond de La Chapelle’.

The towed camera system, Scampi, was used to collect image footage during six cruises (BobGeo, BobGeo 2, and Evhoe 2009, 2010, 2011 and 2012) and acquired photos during 33 dives with a Nikon D700 photo camera. It was looking vertically downwards and therefore perpendicular to the seafloor. Photos were manually taken with intervals of approximately 10 to 90 seconds.

The Remotely Operated Vehicle (ROV) Victor6000 acquired the image footage on 13 dives during the BobEco cruise. This ROV is equipped with multiple cameras, including a Sony FCB-H11 video camera directed vertically. This camera has been used during this study. Frame-grabs have been taken with an interval of approximately one minute, to be able to compare the ROV video with the still images of the towed camera system. Hereafter, we will use the term ‘images’ to refer to both frame-grabs of the ROV and the photos of the Scampi.

Navigation via USBL, timecodes of the videos/photos as well as the georeferencing information were gathered in the software ADELIE (Ifremer). Detailed navigation using the USBL was lacking on the Evhoe cruises (16 dives), so ship navigation was used to georeferenced the images acquired on these cruises.

Most dives followed a depth gradient, because this was the most practical direction. The preferred direction of the Scampi is from shallow to deep waters regarding the potential steep topography and the speed of the winch. The dives with a depth gradient also covered most different geomorphologies in the canyon. The ROV was mostly moving upwards the canyon flank.

Table 1: Dive information including cruise name, year, dive code, canyon, latitude and longitude (median), length measured in 3D, minimum and maximum water depth of the dives, the total number of exploitable images and the number of images on which coral habitats were observed.

Cruise	Year	Dive code	Canyon	Latitude	Longitude	Length (km)	Min depth	Max depth	No. images Total	Total no. images	No. images coral habitats
BobGeo	2009	BG1_1	La Chapelle*	47.5972543	-7.3018781	1.61	224.7	352.3	103	92	0
		BG1_2	La Chapelle*	47.5689723	-7.3459289	2.92	417.4	1076.0	193	154	28
		BG1_3	La Chapelle*	47.5898404	-7.3593201	0.45	439.2	546.2	21	19	0
		BG1_4	La Chapelle*	47.5771639	-7.3609736	1.59	574.9	1039.0	111	97	46
		BG1_5	Morgat	47.3881001	-6.4512668	3.68	421.3	1200.4	310	280	68
		BG1_6	Morgat	47.3647983	-6.4366369	0.79	580.2	854.8	94	79	42
		BG1_7	Odet	46.7841307	-5.1649952	2.74	649.0	1309.3	243	187	171
		BG1_8	Odet-Blavet	46.7400293	-5.0418340	2.64	292.4	396.5	215	173	0
		BG1_9	Odet	46.7880887	-5.0518116	2.03	550.4	952.5	167	140	0
		BG1_10	Odet	46.7803604	-5.2221504	1.28	631.4	898.5	94	83	15
		BG1_11	Belle-île	46.4822928	-4.7384651	2.05	427.0	984.0	151	143	30
Evhoe	2009	EVH09_1	Shamrock	48.1623919	-8.4591893	4.84	185.5	199.9	299	299	0
		EVH09_2	Shamrock	48.1462677	-8.4910439	1.12	199.9	213.0	113	111	0
		EVH09_3	Petite-Sole	48.1317020	-8.8065981	3.42	654.1	986.6	747	691	569
BobGeo 2	2010	BG2_1	Ars	45.6471834	-3.5535464	3.62	470.4	1192.3	216	207	8
		BG2_2	Arcachon	44.3973083	-2.4176186	2.69	1103.7	1533.6	159	151	16
		BG2_3	Arcachon	44.3717064	-2.4282195	1.18	1261.9	1516.0	83	76	6
		BG2_4	Arcachon	44.3298353	-2.2306230	3.82	768.1	1085.0	184	171	55
		BG2_5	Odet-Guilvinec	46.8720076	-5.2427669	0.74	227.5	229.9	61	54	35
		BG2_6	Odet	46.8271589	-5.2687434	5.73	349.9	1170.5	370	352	37
Evhoe	2010	EVH10_1	Blavet	46.6301345	-4.8558125	5.77	280.5	410.5	356	334	48
		EVH10_2	Odet	46.8149943	-5.1739369	2.50	250.1	484.0	209	187	0
		EVH10_3	Hermine	47.8661239	-8.0250322	3.32	387.9	1344.4	268	230	70
		EVH10_4	Hermine	47.8277152	-8.1472261	2.40	1029.4	1854.4	215	195	17
BobEco	2011	BE_465	Rochebonne	45.7780478	-3.7746150	3.58	580.0	1487.4	295	134	1
		BE_466	Ars	45.6798080	-3.6225145	3.02	518.3	1130.8	307	171	2
		BE_467	Saint Nazaire	46.2535308	-4.4086068	2.57	1130.4	1761.8	296	126	9
		BE_468	Croisic	46.3814420	-4.6793497	4.07	708.9	1050.7	337	244	159
		BE_469	Guilvinec	46.9327758	-5.3597874	4.87	803.9	953.2	624	294	271
		BE_470	Lampaul	47.5633329	-7.5321780	11.88	1069.3	2665.5	1092	626	40
		BE_471	Petite-Sole	48.1368207	-8.8111888	8.17	674.6	989.7	527	452	142

		BE_472	Sorlingues	48.1218030	-9.1480668	3.42	1066.4	2323.0	271	168	46
		BE_476	Petite-Sole	48.1201765	-8.8119502	2.68	939.5	959.3	241	191	122
		BE_477	Sorlingues	48.1783925	-9.0844680	9.34	375.7	1232.1	709	587	103
		BE_478	Lampaul	47.6230440	-7.5284670	9.39	506.8	1245.1	891	500	127
		BE_479	Crozon	47.3877187	-6.6237915	10.26	692.4	1382.0	577	491	361
		BE_480	Morgat-Douarnenez	47.3061795	-6.3521557	8.85	713.9	1204.1	491	386	277
Evhoe	2011	Evh11_2	Douarnenez	47.3191960	-6.2723000	3.97	559.0	1577.9	622	594	97
		Evh11_3	Guilcher	47.5076895	-7.1311674	4.76	437.6	1647.9	694	673	233
		Evh11_4	Blackmud	47.8193228	-7.6824182	5.26	557.6	1223.1	712	671	287
Evhoe	2012	Evh12_3	Cap-Ferret**	44.7941036	-2.2029170	7.50	523.0	1913.5	1250	1098	2
		Evh12_4	Athos	45.0544300	-2.8789364	10.34	309.0	2539.2	1119	1001	47
		Evh12_5	Pornic	46.2346696	-4.3360429	3.31	598.7	1329.7	752	693	315
		Evh12_7	Brest	47.4702872	-6.8970797	4.06	451.6	1480.5	593	429	52
		Evh12_8	Shamrock	48.0753351	-8.3109878	3.82	585.0	1126.4	666	480	221
		Evh12_9	Sorlingues	48.2265612	-9.2667409	4.41	232.4	858.4	611	360	16

* The canyon where these dives were performed, north of the Épiron Ostrea, does not have a name. We will use “La Chapelle” to refer to this canyon, using the same term as the sandbank on the continental shelf near this canyon.

** Cold-water coral habitat was present in Cap-Ferret Canyon, but none of these images were selected for the associated fauna analysis

2.3. Image analysis

2.3.1. Quality control and subset

Before analysis, all images were controlled for quality. Images were included in the analyses if they did meet all of the following criteria: (i) altitude of the vehicle to the seafloor was between 1 and 5 m; below 1 m or more than 5 m the vehicle was either too close or too far from the seafloor, (ii) images with a good visibility; images with an obscured view, due to sediment clouds, low light conditions, or high turbidity were excluded from analysis, and (iii) images taken when the vehicle was moving; image taken at a stationary phase of the vehicle (ROV only) were excluded from analysis.

Of the 14,874 images that passed the quality control, 4191 images belonged to one of the 11 coral habitats (Van den Beld *et al.*, 2017). One coral habitat occurred only once and was therefore removed from analysis, resulting in a total of ten coral habitats that are analysed in this study. Of the 4191 images, a subset of 2350 images was annotated for substrate cover and species composition. The subset was created by selecting images with an interval of approximately 1 minute from the start of the dive. For the Scampi photos, taken manually and therefore at irregular time intervals, a buffer of approximately 15 seconds before and after this time interval was considered.

2.3.2. Substrate types

Three categories will be used in this present study: hard substrate, soft substrate and biogenic substrate. The biogenic substrate cover includes the reef-building species *L. pertusa*, *M. oculata* and *S. variabilis*. Van den Beld *et al.* (2017) gives a more detailed description of these measurements.

2.3.3. Megafaunal identification

Organisms were identified until the lowest taxonomic level possible. Taxa were identified as morphotypes and given an Operational Taxonomic Unit (OTU), since it is difficult to identify organisms until species level in the deep sea, mainly due to the lack of specimens that could be identified based on morphological characteristics or genetics. A catalogue was used as a useful guide in identification of the associated fauna (Howell and Davies, 2010; <http://www.marlin.ac.uk/deep-sea-species-image-catalogue>). This guide has been updated as part of a collaborative project between Plymouth University, Ifremer and NOAA. Observed morphotypes that were not yet in the catalogue, have been added in a similar way, giving them a consecutive OTU number. Morphotypes that could consistently be recognised on the image footage, but of which the phylum was not known, were recorded as Unknown sp. #. This is not to be confused with the unidentified organisms that could not be recognised and thus identified at all, because of various reasons, e.g. the size of the organism combined with the altitude of the optical technique. A number of morphotypes are on a low taxonomic level and probably include multiple species, e.g. 'Crustacea spp.' or 'Echinoidea spp.'. These broad morphotypes

were removed from any diversity measurements. Identifications of crinoids, asteroids and squaliformes (sharks) have been done or confirmed by taxonomic experts using voucher specimen or representative images (see acknowledgements). Even though a large number of morphotypes were established, it cannot be excluded that some morphotypes include more than one species, as discriminating differences between species can be so small that they cannot be seen on images, e.g. *Lophius budegassa* and *Lophius piscatorius* (Whitehead *et al.*, 1986b). We are also aware of the risk of misidentifications by and between observers (Durden *et al.*, 2016); however, the use of only one trained observer in this study reduces this risk.

The focus of this study are organisms associated with coral habitats, and therefore only individuals that do not belong to the coral orders Antipatharia, Scleractinia, Alcyonacea and Pennatulacea, are considered as ‘associated fauna’. The term ‘associated fauna/community’ here means all the megafauna that could be observed on images that were tagged as belonging to a coral habitat.

Besides the identification and enumeration of the morphotypes, the substrate type to which the morphotype was attached to was recorded. In the case of motile animals, such as echinoids, crustaceans and fish, the substrate type on which these species were sitting on, i.e. touching, was recorded. Differences were made for fish, between their occurrences in the water column, or under or next to a three-dimensional object from a geological or biological origin (excluding reef-building species *L. pertusa*, *M. oculata* and *S. variabilis*).

2.4. Data treatment

2.4.1. Feeding modes

Feeding modes have been established for each morphotype. The trophic groups used by Bowden *et al.* (2016) have been used for reference, completed by the trophic guilds used by Rowden *et al.* (2010). Suspension and filter-feeder were not distinguished in the present study, since it was not clear for some morphotypes whether they actively pump water to trap particles (suspension-feeder) or passively trap particles suspended in the water (filter-feeders) (Bowden *et al.*, 2016). For species that were not included in either one of these references, the feeding information was extracted from Jumars *et al.* (2015) for polychaetes, Shepard *et al.* (1986) for Ceriantharia, Whitehead *et al.* (1984, 1986a, b) for fish and the World Register of Marine Species (WORMS; www.marinespecies.org).

2.4.2. Environmental data

Depth values were extracted to each image from the bathymetry with a 100m resolution in ArcGIS, prior to the calculation of the mean water depth per habitat segment. A habitat segment is defined as all the adjacent images of the same habitat, until another habitat is allocated to an image.

2.5. Statistical analysis

Each habitat segment was characterized by the mean number of specimens, i.e. density, and the mean number of morphotypes, i.e. mean richness, per image. The densities were given in individuals per image, because the optic vehicles were not equipped with lasers and the altimeter of the Scampi is not reliable enough to calculate the densities based on a surface. Differences in mean densities and mean richness between coral habitats have been tested by a Kruskal Wallis test, followed by the Dunn's test (Dunn, 1964) with a Bonferroni-correction for pairwise comparisons.

Individual-based rarefaction curves with extrapolation using Hill numbers (Chao *et al.*, 2014), the Hurlbert's diversity index, ES_n (Hurlbert, 1971) and the Chao I index (Chao, 1984) were determined per habitat. The ES_n gives the expected species richness in randomised subsamples of n individuals of the different habitats, allowing to compare diversity between habitats based on the same number of individuals (Hurlbert, 1971). This diversity index is thus not dependent on the sample size (Soetaert and Heip, 1990) and can be used in studies with unequal sample-sizes. Chao 1 is a non-parametric species estimator that uses the number of singletons in a sample to extrapolate the number of unsampled species and estimate the true species diversity of an assemblage (Chao *et al.*, 2014).

Beta-diversity, the variation in species composition of the coral habitats, was estimated by calculating the Sørensen (β_{SOR}) index using presence-absence data (Baselga, 2010; Legendre, 2014). The Sørensen distance gives a greater weight to species common to the habitats than those species found in only one habitat. This index accounts for the species nestedness (β_{SNE}) and species turnover (β_{SIM}) between species compositions (Baselga, 2010; Koleff *et al.*, 2003). Nestedness means that the species composition of a smaller sample size is a subset of a species composition of a larger sample size, whereas species turnover means the replacement of species by other species (Baselga, 2010).

Species compositions were analysed by a Principal Component Analysis (PCA). Abundance data were Hellinger-transformed prior to analysis to give a lower weight to dominant taxa (Legendre and Gallagher, 2001). Differences in Hellinger-transformed species compositions between the habitats were tested by a permutational Manova (PERMANOVA) test using 999 permutations.

Spearman correlations have been performed to investigate the relation between biogenic substrate cover or coral density and the density or mean richness of the associated fauna.

The preferences of organisms in attachment substrate, patterns in feeding modes of the different habitats and the preferences of those feeding modes for a certain attachment substrate type, were investigated using descriptive statistics.

All analyses were done in the freely available statistical software R using the 'vegan' (Oksanen *et al.*, 2016), 'betapart' (Baselga *et al.*, 2013), 'ade4' (Dray and Dufour, 2007) and 'dunn.test' (Dinno, 2016) packages. Some figures were created using the ggplot2 package (Wickham, 2009).

3. Results

3.1. *Species densities and dominance patterns*

A total of 32,589 individuals were observed, of which 31,127 individuals could be assigned to a morphotype (95.5%) (Table 2).

The highest density of associated fauna was observed on mixed corals HS (61.4 ± 71.8 individuals/image) (Fig 1A; Table 2). The lowest densities were observed on mixed corals SS (2.7 ± 1.3 individuals/image) and solitary scleractinians SS (3.3 ± 2.0 individuals/image) (Fig 1A; Table 2). Densities differed significantly among habitats (Kruskal Wallis: $\chi^2 = 118.53$, $df = 9$, $p < 0.0001$) and were driven by higher densities on both mixed corals HS and reef habitat. Significantly higher densities were observed in the mixed coral HS habitat than on rubble, colonial scleractinians on both substrate types, solitary scleractinians SS, seapens SS and mixed corals SS (Dunn's post-hoc test: $0.0001 \leq p \leq 0.05$). Significantly higher densities were observed on reef habitat than on the other colonial scleractinian habitats (rubble: $p \leq 0.01$; colonial scleractinians HS: $p < 0.05$; colonial scleractinians SS: $p \leq 0.01$) as well as on seapens SS ($p \leq 0.01$).

Comparing the three groups of habitats based on dominant substrate, higher density was observed in coral habitats on hard substrate (50.8 ± 86.9 ; median = 10.6), followed by biogenic habitats (11.9 ± 16.7 ; median = 6.0) and the lowest densities were observed on soft sediment dominated habitats (4.9 ± 4.2 ; median = 4.0) (Fig 1B). These densities differed significantly (Kruskal Wallis: $\chi^2 = 33.209$, $df = 2$, $p < 0.0001$; Fig 1B). Post-hoc tests show that each of the pairwise comparisons were significantly different ($p < 0.01$).

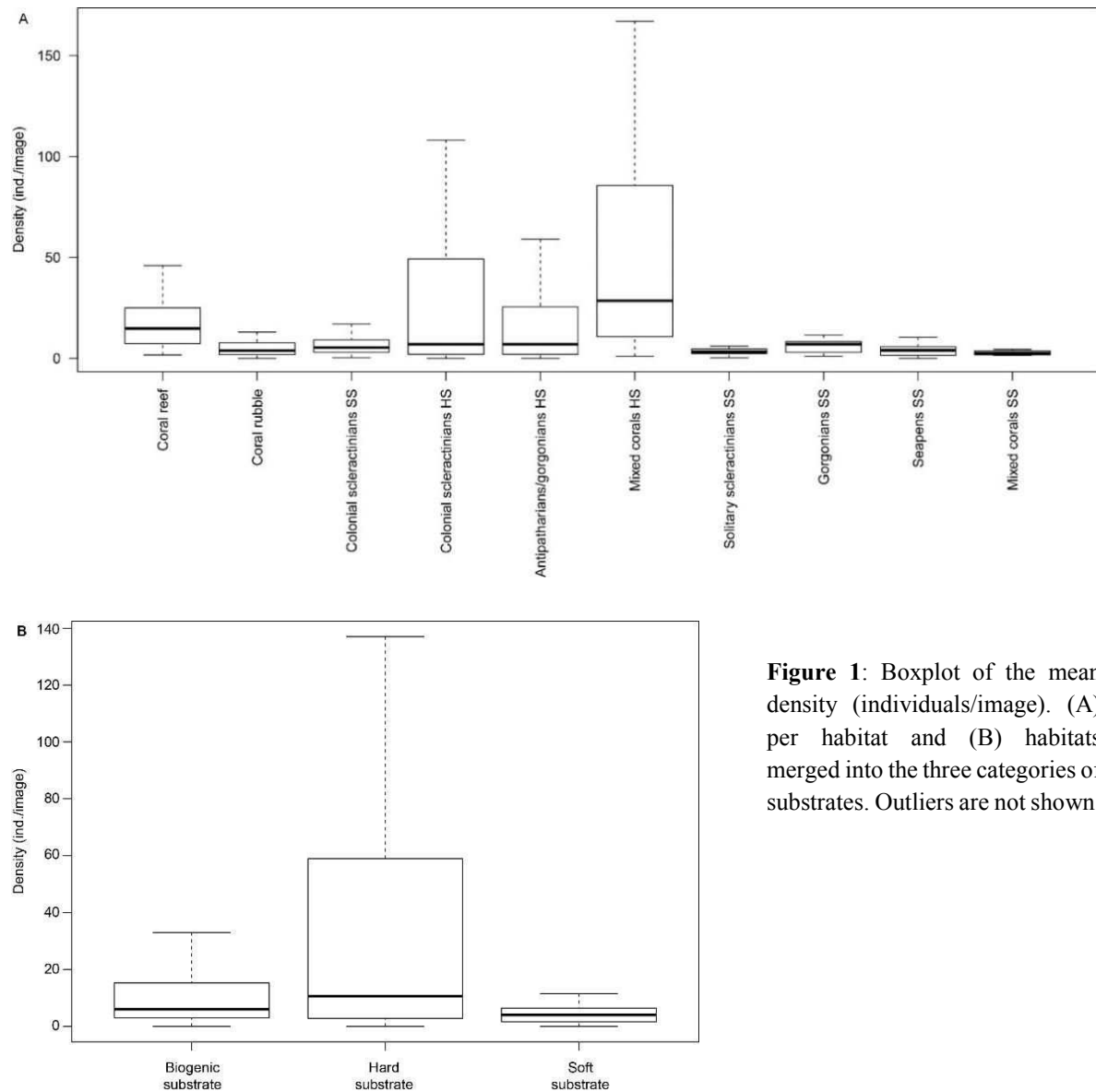


Figure 1: Boxplot of the mean density (individuals/image). (A) per habitat and (B) habitats merged into the three categories of substrates. Outliers are not shown.

Table 2. Abundance, density and diversity of the fauna associated with 10 coral habitats. The percentage of the abundances that was identified to a morphotype is mentioned. The mean densities (individuals per image) and mean richness (richness per image) of each habitat are calculated by averaging the densities or richness per image between the segments (standard deviation between brackets). To compute the species richness and diversity index, the unidentified species and the morphotypes identified on a low taxonomic level have been removed from analysis, resulting in a potential maximum richness of 160 morphotypes. Expected species richness, ES_n (Hurlbert, 1971), is based on 28 individuals. Chao I diversity gives the estimated number of species, based upon the number of rare morphotypes (standard error between brackets). HS = hard substrate; SS = soft substrate.

Coral habitat	Number 'subset' images	No. segments	Total abundance	Identified morphotypes (percentage)	Mean density	Median density	Mean richness per image	Total species richness	Chao I diversity index	ES_{28}
Coral reef	611	106	12481	95.8	19.1 (± 18.7)	14.8	1.9 (± 1.7)	84	96.7 (± 7.5)	8.7
Coral rubble	883	162	4684	93.4	8.7 (± 16.1)	3.9	1.2 (± 1.4)	76	90.3 (± 8.7)	10.8
Colonial scleractinians SS	236	68	1865	96.2	8.3 (± 10.4)	5.3	1.7 (± 1.7)	45	72.2 (± 18.2)	8.4
Colonial scleractinians HS	185	49	5043	98.5	46.0 (± 81.6)	7.0	1.4 (± 1.3)	49	58.8 (± 7.2)	6.0
Antipatharians/gorgonians HS	30	24	899	88.5	42.1 (± 120.1)	7.0	1.7 (± 2.2)	24	29.3 (± 5.4)	5.9
Mixed corals HS	92	43	6596	97.0	61.4 (± 71.8)	28.6	2.5 (± 1.4)	51	58.1 (± 5.3)	4.2
Solitary scleractinians SS	21	6	63	96.8	3.3 (± 2.0)	3.3	0.8 (± 0.4)	10	17.5 (± 8.1)	8.8
Gorgonians SS	24	14	167	96.4	7.0 (± 5.5)	7.0	1.9 (± 1.2)	22	31.0 (± 8.0)	11.0
Seapens SS	257	54	752	78.6	4.3 (± 4.0)	4.0	1.0 (± 0.9)	59	91.5 (± 17.2)	12.2
Mixed corals SS	11	5	39	89.7	2.7 (± 1.3)	2.5	1.4 (± 1.1)	12	19.0 (± 7.1)	12.0
Total	2350	532	32589	95.5	18.6 (± 43.9)	6.3	1.6 (± 1.5)	160	-	-

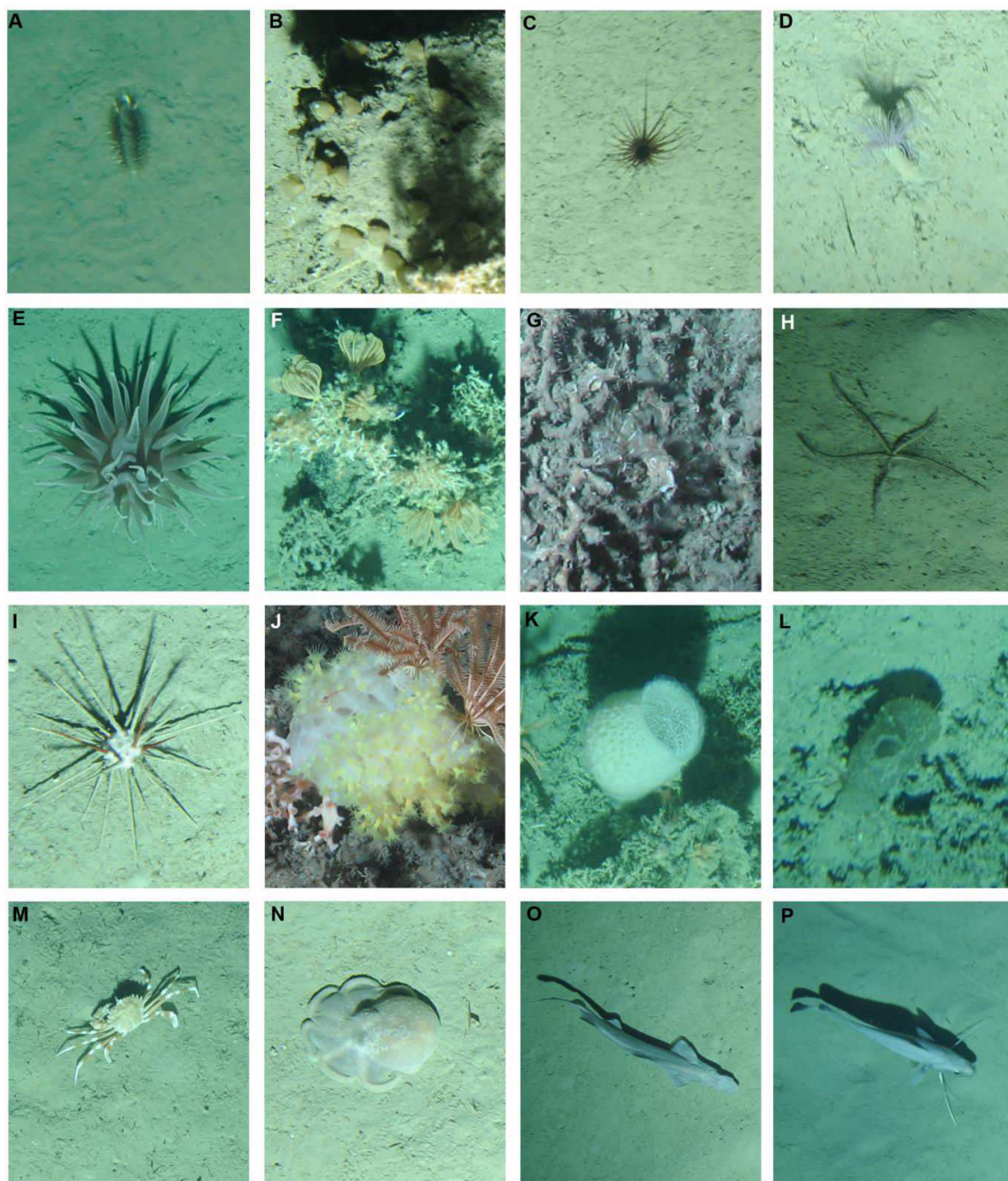


Figure 2: Example images of morphotypes: (A) Aphroditidea sp. 1 (Annelida) (Evhoe 2011); (B) Brachiopoda sp. 1 (Evhoe 2011); (C) Cerianthidae sp. 1 (Cnidaria, Ceriantharia) (BobGeo 2, 2010); (D) Cerianthidae sp. 4 (Cnidaria, Ceriantharia) (Evhoe 2010); (E) *Bolocera* sp. 1 (Cnidaria, Actiniaria) (BobGeo 2, 2010); (F) *Koehlermetra porrecta* (Echinodermata, Crinoidea) on a live *Lophelia pertusa* colony (Cnidaria, Scleractinia) (BobGeo 2, 2010); (G) *Neocomatella europeae* (Echinodermata, Crinoidea) between dead *Lophelia/Madrepora* framework (BobEco, 2011); (H) *Pentametrocrinus atlanticus* (Echinodermata, Crinoidea) (BobGeo 2, 2010); (I) *Cidaris cidaris* (Echinodermata, Echinoidea) (Evhoe 2011); (J) Zoanthidae sp. 3 (Cnidaria; Zoantharia) on *Aphrocallistes beatrix* (Porifera, Hexactinellida). Two specimens of *K. porrecta* are on the top right and a live *Lophelia pertusa* colony on the bottom left (BobEco, 2011); (K) *Euplectella* sp. 1 (Porifera, Hexactinellida) (Evhoe, 2009); (L) Unknown sp. 42 (BobGeo, 2009); (M) *Bathynectes* sp. (Arthropoda, Decapoda) (BobGeo 2, 2010); (N) a cephalopod species (Mollusca, Cephalopoda) (Evhoe 2011); (O) *Deania* sp. 1 (Chordata, Elasmobranchii) (BobGeo 2, 2010); (P) *Phycis blennoides* (Chordata, Actinopterygii) (Evhoe 2011).

A total of 191 morphotypes were identified to be associated with coral habitats in the Bay of Biscay (Table 2 and 3). Examples of morphotypes are given in Fig 2. The morphotypes belonged to at least ten phyla; the phylum remained unknown for eighteen morphotypes (Table 3). Sixty-two morphotypes were identified until at least genus level (32.5%), including forty-two morphotypes at species level. Thirty-one morphotypes were identified with a low taxonomic resolution to only phylum, order or family name, and could include multiple species. Examples include Gastropoda spp., Crustacea spp. and Porifera spp. The remaining 160 morphotypes are considered to be unique based on visible morphological characters, even though they were not always identified to genus or species level, e.g. *Colus* sp. 2, Decapoda sp. 6 and Cup sponge sp. 3. These 160 morphotypes were used in alpha and beta diversity metrics. The contributions of the phyla to the community composition differed among coral habitats (Fig 3A) driven by one or a few morphotypes (Fig 3B). Brachiopods (Fig 2B) dominated the hard substrate habitats and were composed of only one morphotype. They were also observed in the biogenic coral rubble and colonial scleractinians SS habitats but were not dominating these habitats. Echinoderms, especially the crinoid *Koehlermetra porrecta* (Fig 2F), dominated or co-dominated the biogenic habitats. The cnidarians also contribute significantly to the biogenic habitats, especially on coral rubble where they are dominant. Cerianthidae sp. 1 (Fig 2C) was the most abundant cnidarian in the biogenic habitats, followed by actinian/corallimorph sp. 1, Zoanthidea sp. 3 (Fig 2J), Cerianthidae sp. 4 (Fig 2D) and Ceriantharia sp. 5. Another 22 cnidarian morphotypes were present in the biogenic habitats, but their contribution was small (less than 1.5%).

The dominance patterns were less evident on the soft substrate habitats and the abundances were more equally distributed among these habitats. Cnidarians, echinoderms and gastropods contributed the most to the soft substrate habitats, but were represented by several morphotypes that were Cerianthidae sp. 1, the actinians *Bolocera* sp. 1 (Fig 2E) and *Phelliactis* sp. 1, the crinoids *Pentametrocrinus atlanticus* (Fig 2H) and Crinoidea sp. 2 as well as the asteroids *Nymphaster arenatus*, Brisingida sp. 3 and Brisingida sp. 5. The molluscs, particularly the gastropod *Calliostoma* sp. 1, were abundant on the solitary scleractinians on soft substrate. Chordata, mainly composed of fish, contribute for more than 5% to the compositions on the gorgonians SS (5.5%), sea pens SS (8.0%) and mixed corals SS (7.1%) habitats. The fish were mainly represented by the northern cutthroat eel *Synaphobranchus kaupii* and the shark *Deania* sp. 1.

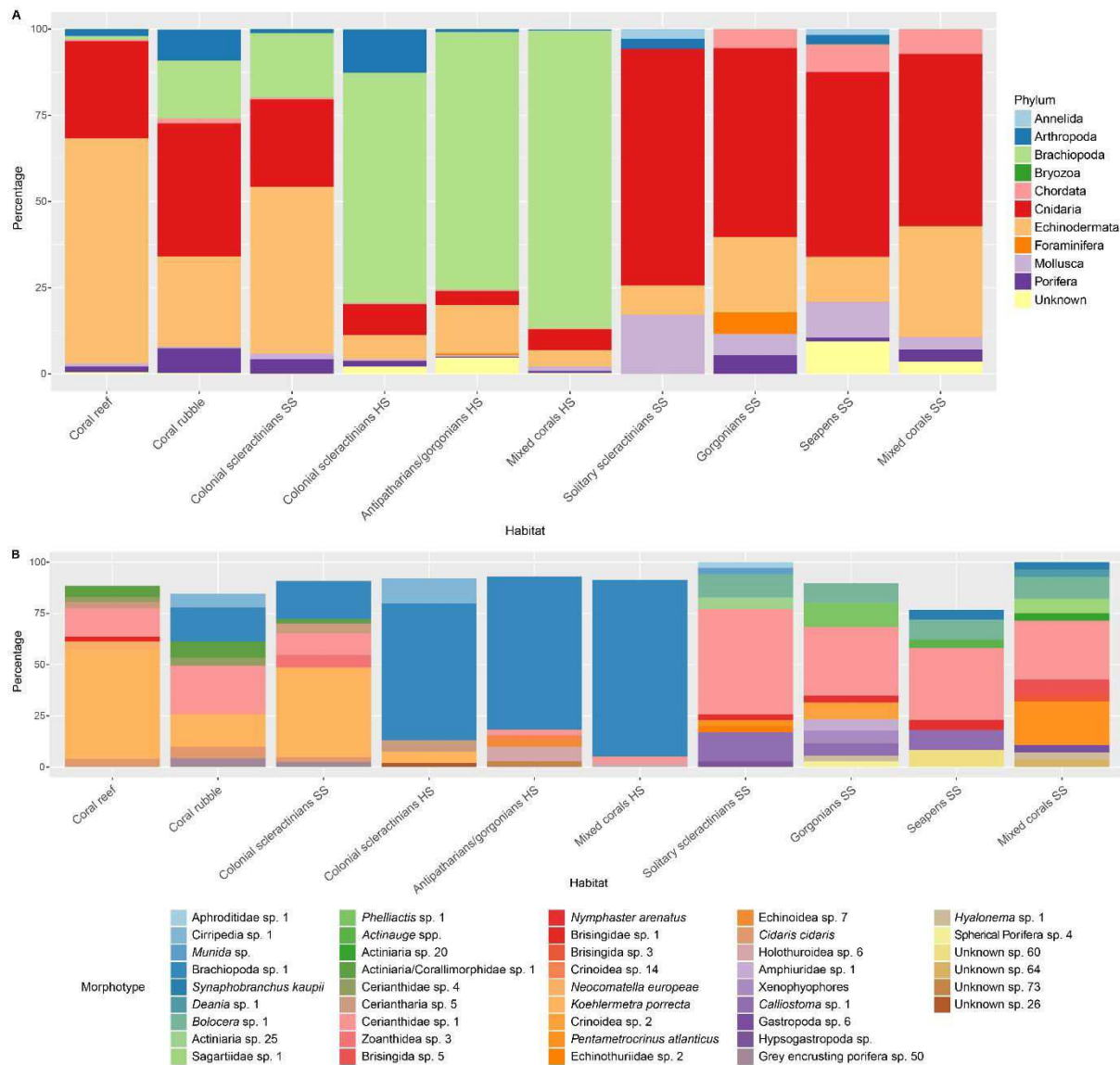


Figure 3: Stacked bar plots with the contributions of phyla (A) and morphotypes (B) to the coral habitats in percentages. In the bar plot of the morpho-types (B) only those morpho-types contributing 2% or more are shown. The species that were not identified are not included.

Table 3. The morphotypes and their abundances observed within the coral habitats of the Bay of Biscay. Feeding mode: FS = filter/suspension feeder, G = grazer, D = deposit-feeder, P = predator/scavenger, U = unknown. The asterisk indicates the morphotypes that were excluded from the diversity analysis, because of a taxonomic resolution that is too low.

Phylum	Class or order	Morpho-type	Feeding mode	Coral reef	Coral rubble	Colonial scleractinians SS	Colonial scleractinians HS	Antipatharians/ gorgonians HS	Mixed corals HS	Solitary scleractinians SS	Gorgonians SS	Seapens SS	Mixed corals SS	Total abundance
Total				12481	4684	1865	5043	899	6596	63	167	752	39	32589
Annelida	Echiuroidea	<i>Bonellia viridis</i>	D	1	10		4		12					27
	Polychaeta	Sabellida spp. *	FS	83	8				11				1	103
		Aphroditidae sp. 1	P							1		8		9
		Serpulidae spp. *	FS	19	4		1		1					25
Arthropoda	Cirripedia	Cirripedia sp. 1	FS		261		595							856
	Crustacea	Crustacea spp. *	P	13	13	2	5	4	6	2	2	20	2	69
	Decapoda	<i>Bathynectes</i> spp.	P	37	26	4	1		6					74
		Caridea sp. 1	P									1		1
		<i>Chaceon affinis</i>	P			2						2		4
		Chirostylidae spp.	P	9			1							10
		Decapoda sp. 6	P									3		3
		Decapoda spp. *	P	6	5	3	1	1			2	8	3	29
		Majidae sp. 1	P	1										1
		Majidae sp. 2	P				1							1
		<i>Munida</i> sp.	P	123	70	12	5	6	8	1		5		230
		Paguridae spp. *	P	1	4		1					6		12
		<i>Pandalus borealis</i>	P	52	2	3						1		58
		<i>Paromola cuvieri</i>	P	2										2
Brachiopoda	Brachiopoda	Brachiopoda sp. 1	FS	125	677	324	3216	559	5407					10308
Bryozoa	Bryozoa	Bryozoa spp. *	FS	14										14
		Cyclostomatida sp. 4	FS									1		1
Chordata	Actinopterygii	Actinopterygii spp. *	P	34	17	2	5	7	13		1	10		89

Elasmobranchii	Alepocephalidae sp. 1	P		1					1			2	
	Anguilliformes spp. *	P		1				1				2	
	<i>Bathypterois</i> sp. 1	P							1			1	
	<i>Capros aper</i>	P								3		3	
	<i>Nezumia aequalis</i>	P		2								2	
	<i>Coryphaenoides rupestris</i>	P							1			1	
	<i>Helicolenus dactylopterus</i>	P	5	2	1	1				2		11	
	<i>Hoplostethus atlanticus</i>	P		2		6		2		1		11	
	<i>Lepidion eques</i>	P	32	15	3	3				1	3	54	
	<i>Lophius</i> spp.	P	1	1							1	3	
	Macrouridae spp. *	P	1	1	1	1	1	2		3	4	1	15
	<i>Merluccius merluccius</i>	P									1		1
	<i>Microchirus variegatus</i>	P									2		2
	<i>Molva dypterygia</i>	P		3									3
	<i>Molva molva</i>	P									1		1
	<i>Mora moro</i>	P	1					1		1	1		4
	Moridae spp. *	P	2		1								3
	<i>Neocyttus helgae</i>	P				2		2					4
	Notacanthiformes sp. 1	P		1		1				1			3
	<i>Phycis blennoides</i>	P	2					1					3
	<i>Synaphobranchus kaupii</i>	P	3	21	5	3	1	11		1	22	1	68
	<i>Trachyscorpia cristulata</i>	P	2	3									5
	Elasmobranchii	<i>Galeus melastomus</i>	P		2			1	1		1		5
		<i>Scyliorhinus canicula</i>	P		1								1
		<i>Deania</i> sp. 1	P									1	1
		Squaliformes sp. 3	P						1				1
		Squaliformes spp. *	P	1									1
	Pisces	Pisces spp. *	P	33	35	6	8			5	4		91
	Tunicata	Ascidiacea sp. 5	FS		3								3
		Ascidiacea sp. 6	FS	2		1							3
		Ascidiacea spp. *	FS	3				1					4
	Cnidaria	Actiniaria	<i>Actinauge</i> spp.	FS		9					18		27

	Actiniaria sp. 4	FS	4										4
	Actiniaria sp. 11	FS	1										1
	Actiniaria sp. 15	FS						1					1
	Actiniaria sp. 20	FS	30	4	2	8	1	5				1	51
	Actiniaria sp. 24	FS	3	1								1	5
	Actiniaria sp. 25	FS		1				3	2			2	8
	Actiniaria sp. 26	FS	151	2	4								157
	Actiniaria spp. *	FS	50	9	8	104		7				2	180
	<i>Bolocera</i> sp. 1	FS	2	31	1	2	2	36	4	14	46	3	141
	<i>Phelliactis</i> sp. 1	FS						1		17			18
	Sagartiidae sp. 1	FS										2	2
	Sagartiidae sp. 5	FS										3	3
Actiniaria/ Corallimorpharia	Actiniaria/ Corallimorpharia sp. 1	FS	624	320	35	5	1	43				1	1029
Ceriantharia	Ceriantharia sp. 5	FS	348	50	84	256	4	57				2	801
	Ceriantharia sp. 6	FS	1	4								3	8
	Cerianthidae sp. 1	FS	1582	954	184	59	20	180	18	49	164	8	3218
	Cerianthidae sp. 4	FS	275	160	19	1		7				4	466
	<i>Pachycerianthus multiplicatus</i>	FS	9	1	2							5	17
	Ceriantharia spp. *	FS	5	30								1	36
Corallimorpharia	Corallimorphidae sp. 2	FS	2										2
Hydrozoa	Hydrozoa bushy	FS					1			1			2
	Hydrozoa flat branched	FS	5										5
	Hydrozoa irregular	FS	1										1
	Hydrozoa sp. 1	FS				2							2
	Hydrozoa sp. 2	FS	3										3
	Hydrozoa sp. 3	FS	17			40	2						59
	<i>Stylaster</i> sp. 1	FS			1								1
	<i>Pliobotrus</i> sp. 1	FS	2	3			1						6
	Hydroids spp. *	FS	40		3			3					46
Zoantharia	Zoanthidea sp. 1	FS	21	6									27
	Zoanthidea sp. 2	FS	79			40							119

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		Stalked crinoidea spp. *	FS	1	1	16	4						22
	Echinoidea	<i>Araeosoma fenestratum</i>	G	3	2						1		6
		<i>Cidaris cidaris</i>	G	447	224	40	36	2	21		3		773
		Echinoidea sp. 6	G								1		1
		Echinoidea sp. 7	G					26					26
		Echinoidea spp. *	G	3	4	1	1	2	4		2		17
		Echinothuriidae sp. 2	G	7	14	4	1		5	1	1		33
		Echinothuriidae spp. *	G	13	37	4	4		6		6		70
		<i>Echinus</i> sp. 1	G	2	2						1		5
		<i>Echinus</i> spp. *	G	3	1		2				1		7
		<i>Phormosoma placenta</i>	G								1		1
	Holothuroidea	<i>Benthogone rosea</i>	D						3				3
		Holothuroidea sp. 6	D					54	138				192
		Holothuroidea spp. *	D		13								13
		<i>Parastichopus tremulus</i>	D		1								1
	Ophiuroidea	Amphiuridae sp. 1	D		3				8		8	3	22
		<i>Asteronyx loveni</i>	FS								2		2
		<i>Ophiactis balli</i>	D		2								2
		<i>Ophiomusium lymani</i>	D								3		3
		<i>Ophiothrix fragilis</i>	D		23								23
		Ophiuroidea sp. 1	D		27						1		28
		Ophiuroidea sp. 2	D			1							1
		Ophiuroidea sp. 11	D					4					4
		Ophiuroidea spp. *	D	3	68	5	3	1	2		20		102
Foraminifera	Xenophyophores	Xenophyophores	FS					4	1		9		14
Mollusca	Bivalvia	Bivalvia spp. *	FS		1								1
		Pectinidae spp.	FS		3								3
	Cephalopoda	Cephalopoda spp. *	P	4							1		5
	Gastropoda	<i>Calliostoma</i> sp. 1	G	86	13	25	10	3	78	5	9	45	274
		Cerithioidea spp.	G			1					1		2
		<i>Colus</i> sp. 2	G	1	2	1	6				1		11
		Gastropoda sp. 1	G	1									1

Porifera		Gastropoda sp. 6	G		1					1	1	3
		Gastropoda spp. *	G	99	29	9	7	3	35	23	40	245
		Hypsogastropoda sp.	G	3		3	4		2	1		13
		Nudibranchia sp. 1	P	1								1
	Demospongiae	<i>Geodia</i> sp. 1	FS	7	3				3		1	14
	Encrusting sponges	<i>Hexadella</i> spp.	FS	3	1				2		1	7
		Blue encrusting sponge sp. 46	FS	33	21	11	15	1	18			99
		Blue encrusting sponge sp. 47	FS	8								8
		Grey encrusting sponge sp. 50	FS	8	172	45	18					243
		Grey/cream encrusting sponge sp. 51	FS	6	1	9	17					33
		White encrusting sponge sp. 52	FS	5	1	1						7
		Yellow encrusting sponge sp. 48	FS	45	72		4		1			122
		Encrusting sponge spp. *	FS	2	3		1		4			10
	Hexactinellida	<i>Aphrocallistes beatrix</i>	FS	49	12	4	4		5			74
		<i>Euplectella</i> sp. 1	FS	12	1	1	1					15
		Hexactinellida sp. 26	FS	3								3
		Hexactinellida spp. *	FS	5	2	1	1		6			15
		<i>Hyalonema</i> sp. 1	FS			1		1		4	1	7
	Porifera	Cup sponge sp. 3	FS				2					2
		Lamellate sponge sp. 1	FS	2			21					23
		Lamellate sponge sp. 3	FS	1	1							2
		Lamellate sponge sp. 7	FS	2								2
		Lamellate sponge sp. 11	FS	2								2
		Massive globose sponge sp. 3	FS						2			2
		Massive globose sponge sp. 9	FS		6							6
		Spherical sponge sp. 4	FS	3	1				3	4	3	14

		Porifera spp. *	FS	7	9	2	2	10	12					42
Unknown	Unknown	Unknown sp. 25	U					8	16					24
		Unknown sp. 26	U	23			100							123
		Unknown sp. 32	U								1			1
		Unknown sp. 42	U	14	1	1	2		5					23
		Unknown sp. 51	U	23	5									28
		Unknown sp. 52	U	1										1
		Unknown sp. 54	U	1										1
		Unknown sp. 55	U			1								1
		Unknown sp. 60	U					7			39			46
		Unknown sp. 61	U								1			1
		Unknown sp. 63	U								2			2
		Unknown sp. 64	U									1		1
		Unknown sp. 66	U								1			1
		Unknown sp. 70	U	2										2
		Unknown sp. 71	U	1										1
		Unknown sp. 73	U					21	1					22
		Unknown sp. 74	U						1					1
		Unknown sp. 75	U		3									3
Unidentified	Unidentified	Unidentified species *	U	530	311	70	75	103	200	2	6	161	4	1462
Total				12481	4684	1865	5043	899	6596	63	167	752	39	32589

3.2. Species richness and alpha diversity

The coral reef habitat had the highest species richness (84 morphotypes), followed by coral rubble (76) and seapens SS (59) (Table 2). The lowest species richness was observed in the habitats mixed corals SS (12) and solitary scleractinians SS (10) (Table 2), but the number of image analysed for each habitat (sampling effort) was different.

The mean richness per image was compared between habitats (Fig 4A; Table 2). The mean richness per image was highest on mixed corals HS (2.5 ± 1.4 morphotypes/image), followed by reef (1.9 ± 1.7 morphotypes/image) and gorgonians SS (1.9 ± 1.2 morphotypes/image) and lowest on solitary scleractinians SS (0.8 ± 0.4 morphotypes/image) and seapens SS (1.0 ± 0.9 morphotypes/image). Overall, the mean richness differed significantly between habitats (Kruskal- Wallis: $\chi^2 = 48.911$, $df = 9$, $p < 0.01$). The richness on mixed corals HS was significantly higher than the richness on coral rubble, colonial scleractinians SS, colonial scleractinians HS and seapens SS ($p < 0.04$). Richness per image was also significantly higher on coral reef than on coral rubble ($p < 0.001$) and seapens SS ($p = 0.02$).

Comparing the habitats based on the dominant substrate type (Fig 4B), the mean richness per image did not differ significantly ($p = 0.06$).

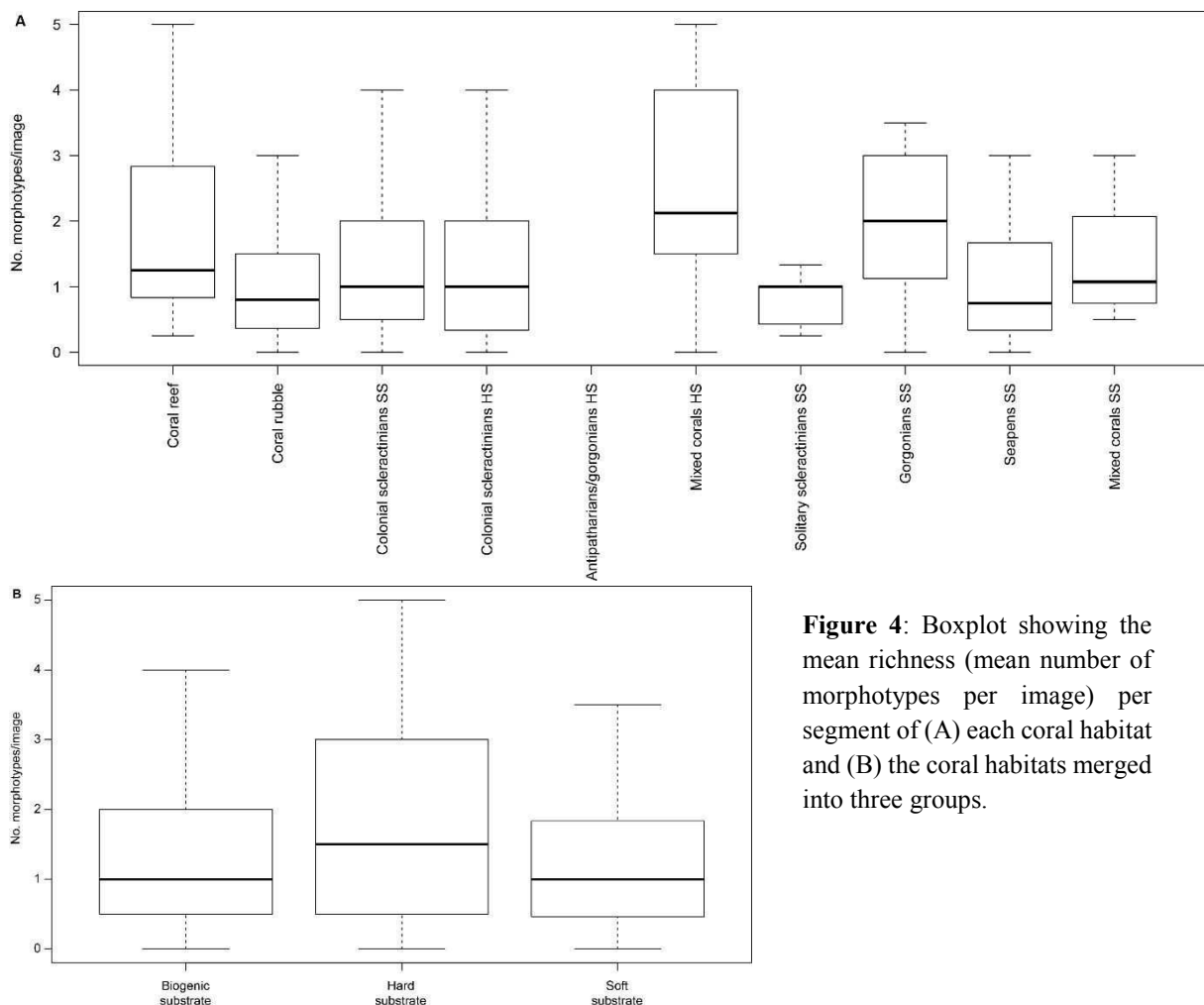


Figure 4: Boxplot showing the mean richness (mean number of morphotypes per image) per segment of (A) each coral habitat and (B) the coral habitats merged into three groups.

The individual-based rarefaction curves tend to an asymptote for four out of ten coral habitats (Fig 5). The biogenic habitats – reef and rubble – have higher expected species richness than the hard substrate habitats formed by colonial scleractinians or a mix of corals. The curve of the colonial scleractinians SS habitat is similar to the curve of the coral reef habitat, although undersampling is manifest. Even though the rarefaction curve of seapens on soft substrate did not reach the asymptote, and the habitat is thus undersampled, the richness of this habitat may be similar or even higher than the richness of the biogenic habitats as well as the hard substrate habitats.

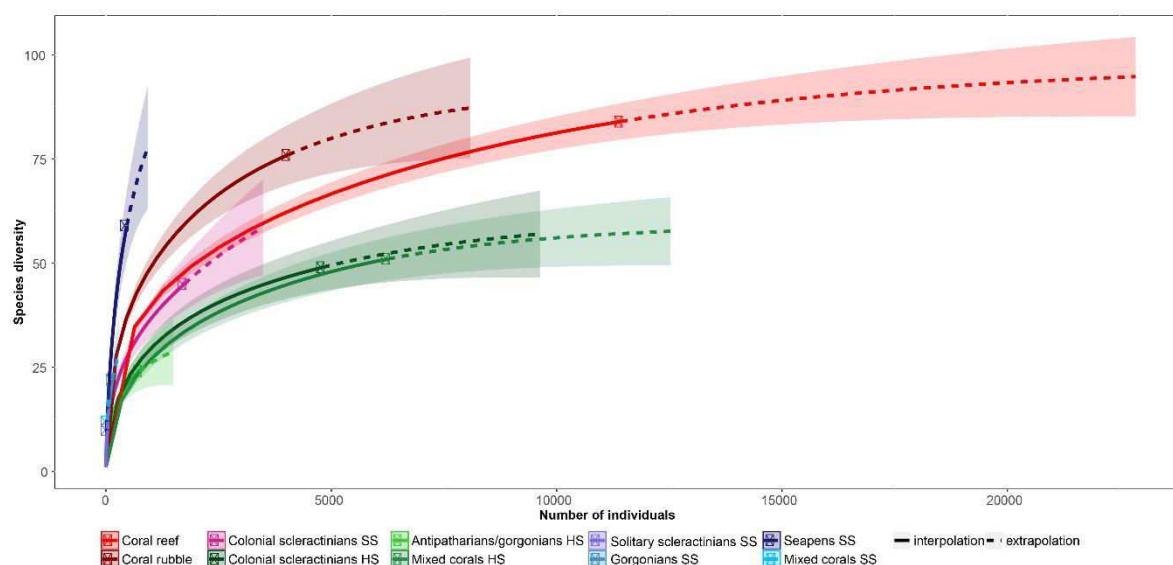


Figure 5: Individual based rarefaction curves of the associated species community in coral habitats. Unidentified species are excluded, but the morpho-types identified as Unknown are included. The Chao I index is used for the extrapolations of the curves (dashed line).

Diversity patterns using the ES₂₈ and the Chao I indices were calculated for each habitat. The ES₂₈ ranged from 4.2 to 12.2 morphotypes and the Chao I index from 18 to 97 species (Table 2). Biogenic habitats have a higher diversity than hard substrate coral habitats according to both indices. Sea pens SS also has a higher diversity than hard substrate coral habitats. In addition, coral reef and rubble have a more diverse community than colonial scleractinians SS, but reef has a higher Chao I index and a lower ES₂₈ index than rubble. The hard substrate habitats have the lowest ES₂₈.

3.3. Beta-diversity and taxonomic composition

Variations in dominance patterns are illustrated in the two first axes of the PCA, which explains 45.4% and 23.1% of the variance respectively (Fig 6). The first axis separated the communities of the coral habitats on soft substrate from the communities of the other CWC habitats. The second axis separated the biogenic habitats from the habitats on hard substrate. Even though colonial scleractinians HS was formed by colonial scleractinians that also form the biogenic habitats, the species community is more similar to the other hard substrate coral habitats than the biogenic habitats. This was due to the characterising species of this habitat, Brachiopoda

sp. 1, which is observed in large numbers in coral habitats on hard substrate. The crinoid *K. porrecta* is characterising the biogenic habitats. Coral habitats on soft substrate were characterised by the cnidarians *Bolocera* sp. 1 (Actiniaria) and Cerianthidae sp. 1 (Ceriantharia). Other species that characterise the different groups of habitats were Holothuridea sp. 6 on hard substrate habitats, Actiniaria/Corallimorpharia sp. 1, Cerianthidae sp. 4, *Neocomatella europeae* (Crinoidea; Fig 2G) and *Cidaris cidaris* (Echinoidea; Fig 2I) on biogenic habitats and *Pentametrocrinus atlanticus* (Crinoidea; Fig 2H) and *Calliostoma* sp. 1 (Gastropoda) on soft substrate habitats. Species composition differed significantly between habitats (PERMANOVA; $p = 0.001$).

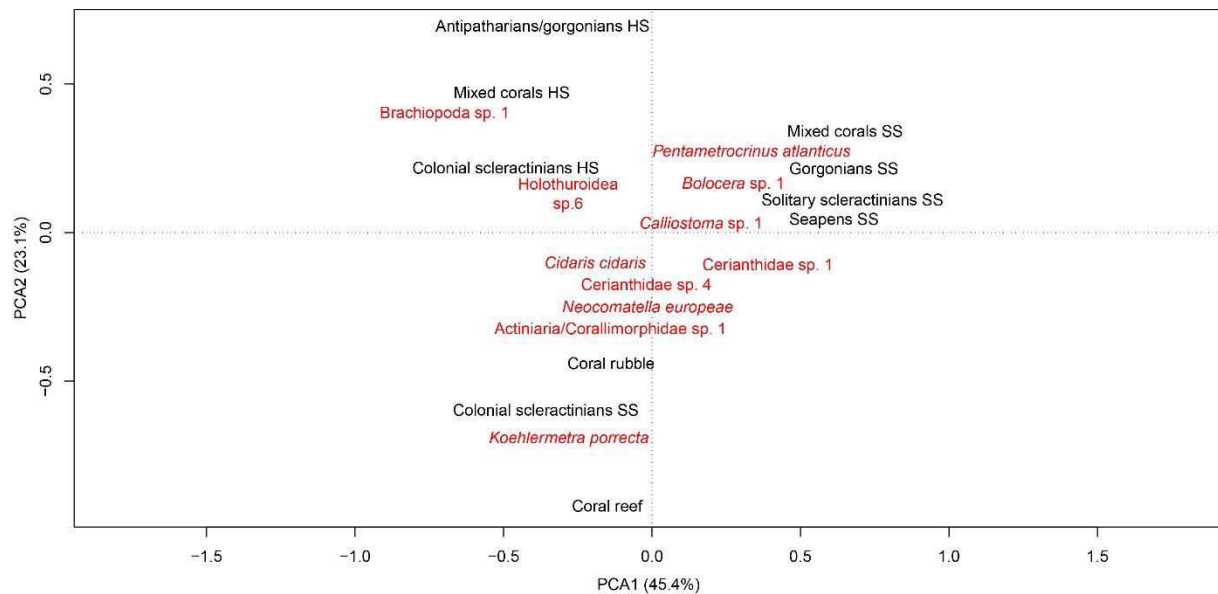


Figure 6: Principal Component Analysis of the Hellinger-transformed abundances of morphotypes observed in each coral habitat. Only morphotypes contributing for 2% to the variation in the data are displayed.

Beta diversity indices

The overall beta-diversity between all habitats, using presence-absence data, was high, with an estimated Sørensen-based multiple-site dissimilarity of 81.8% and was mainly caused by species turnover (66.0%) rather than nestedness (15.8%). The dissimilarity between the habitats merged into three substrate categories was lower, reaching a dissimilarity of 56.2%, mainly caused by nestedness (81.9%) rather than species turnover (48.0%).

The species-occupancy frequency distribution showed that half of the species occupied either one (68 morphotypes, 43%) or two habitats (27 morphotypes, 17%) (Fig 7). Only two morphotypes (1.3%) – *Bolocera* sp. 1 and Cerianthidae sp. 1 – were observed in all ten coral habitats.

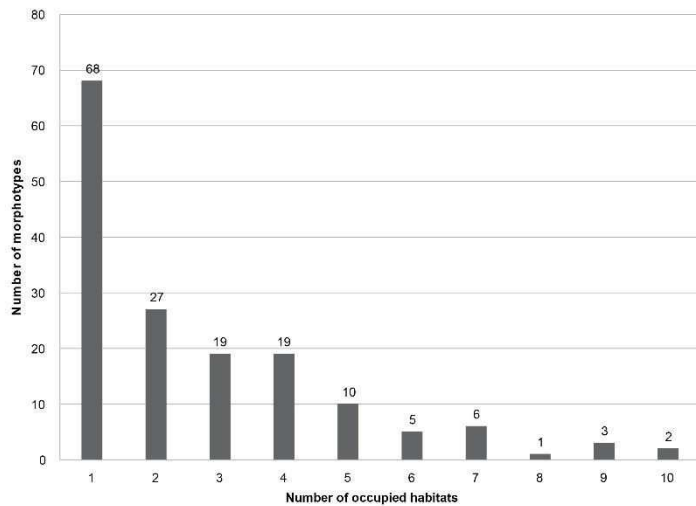


Figure 7: The species-frequency occupancy distribution. This graph shows the number of morphotypes (y-axis) occupying one or more habitats (x-axis).

The Venn diagram shows the distribution of morphotypes according to habitat types (Fig 8). Eighteen percent of the morphotypes, corresponding to 28 morphotypes, were shared among all 3 substrate types, while 41 morphotypes (26%) were unique to biogenic habitats, 26 (16%) were unique to soft-sediment habitats and 18 morphotypes (11%) were unique to hard substrate habitats. Biogenic habitats shared 17 morphotypes (11%) with soft sediment habitats and 26 morphotypes (14%) with hard substrate habitats, while only 4 morphotypes (3%) were shared between hard and soft habitats.

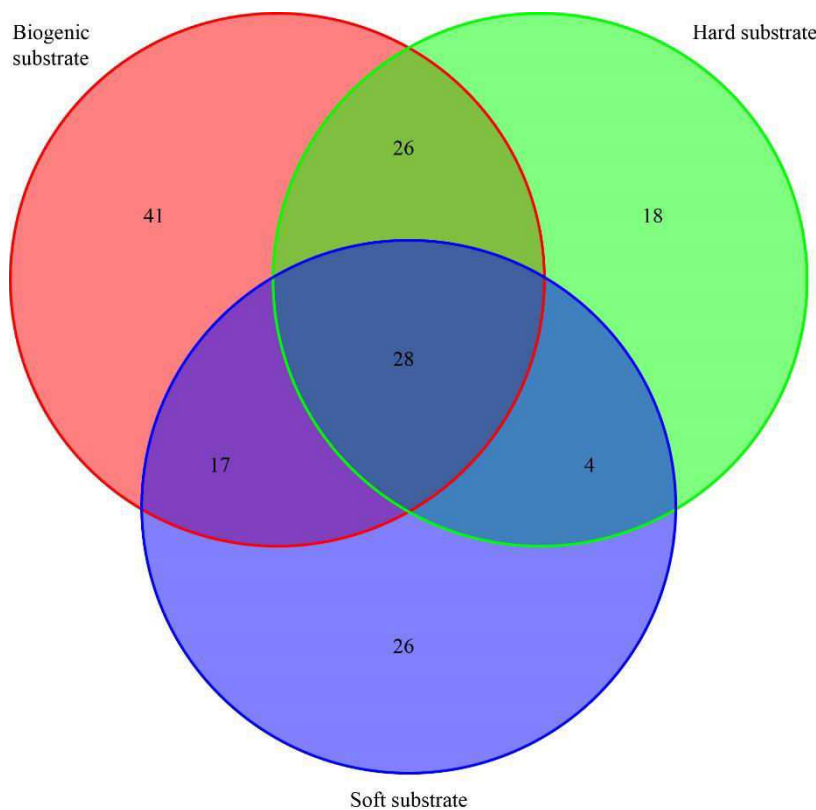


Figure 8: A Venn diagram. It shows the number of shared and unshared morphotypes between habitats per dominant substrate type. Biogenic habitats are in red: reef, rubble and colonial scleractinians SS; Hard substrate habitats are in blue: colonial scleractinians HS, antipatharians/gorgonians HS and mixed corals HS; Soft substrate habitats are in green: solitary scleractinians SS, gorgonians SS, seapens SS and mixed corals SS).

3.4. Influence of cold-water corals on associated fauna

Correlations were computed for all habitats segments in order to test the relationships between biogenic substrate cover or coral densities and the density or richness of the associated fauna (Fig 9A). The spearman correlation tests show significant correlations but the correlation coefficients are low and the scatter plots do not reveal any consistent patterns. At the scale of the ten habitats however, the diversity of the associated species (ES₂₈) is significantly and negatively correlated with the diversity of coral species (ES₁₆) (Fig 9B).

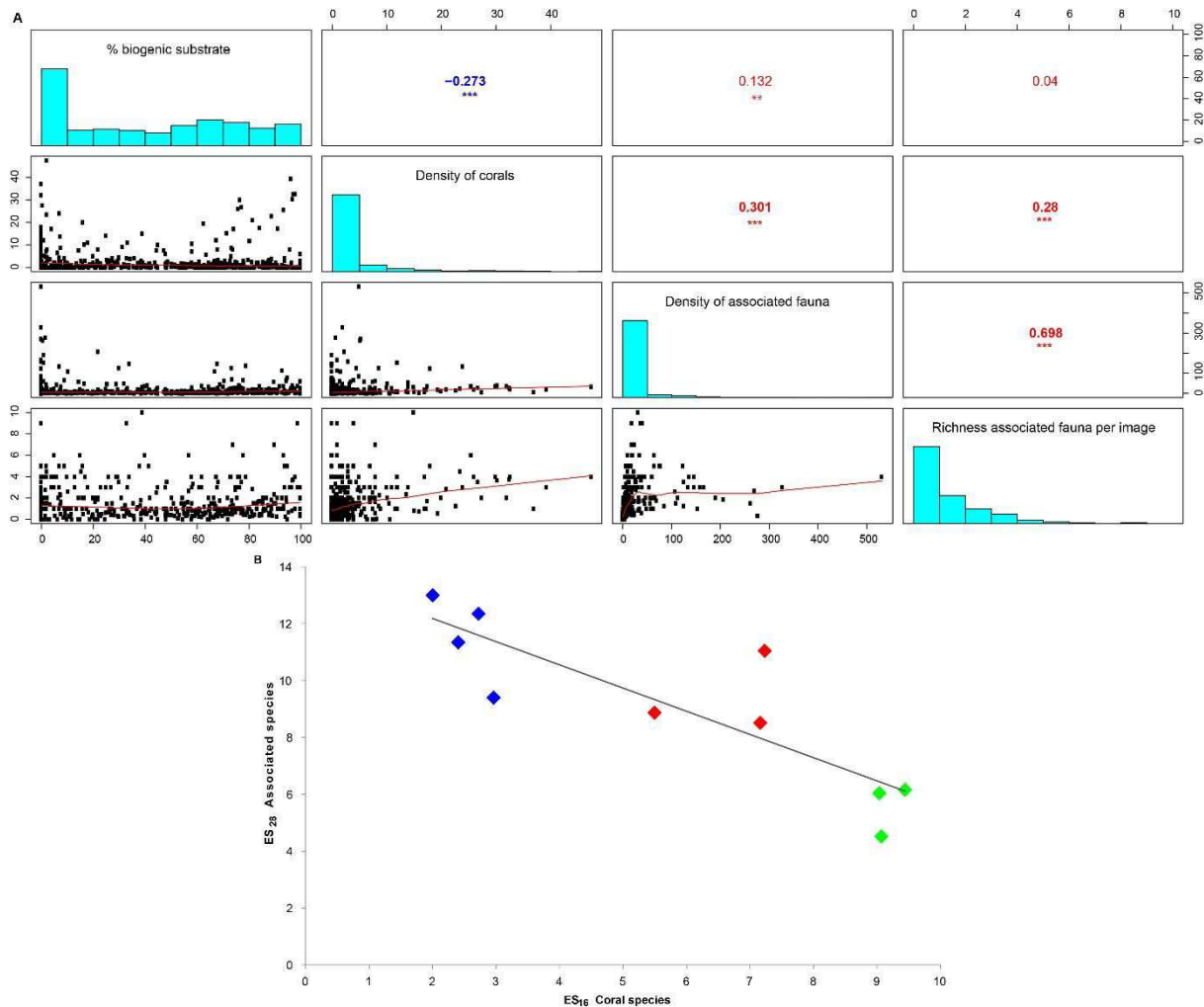
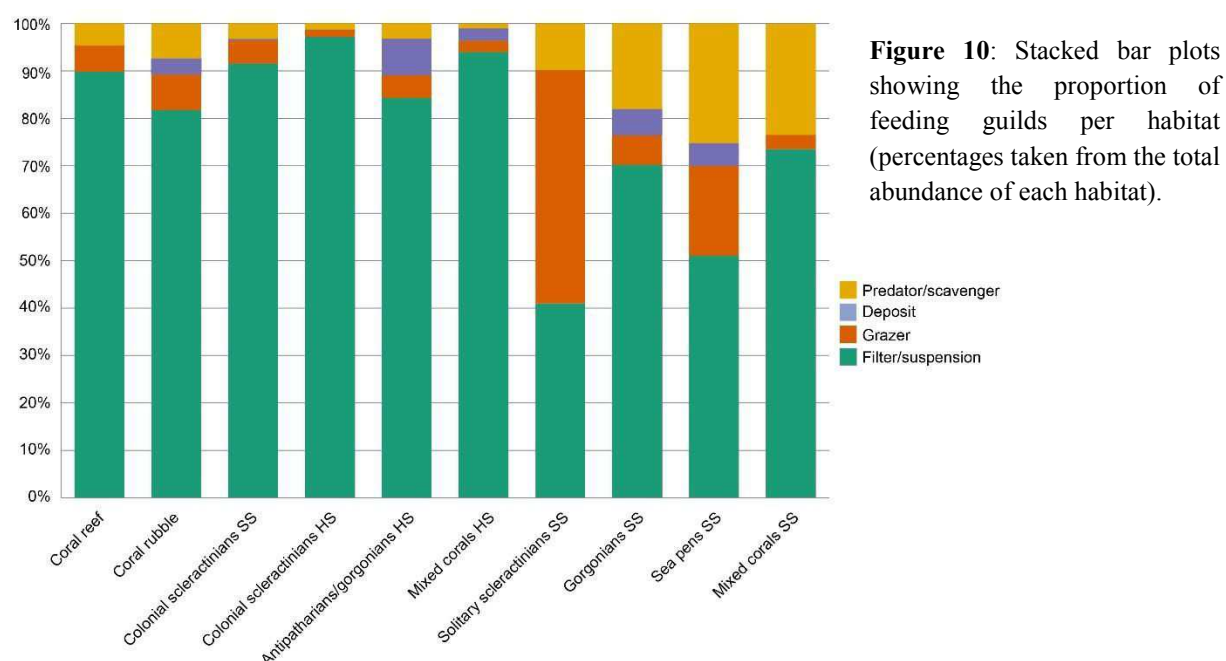


Figure 9: The influence of cold-water corals on the associated fauna. (A) Correlation matrices between coral cover (reef-building scleractinians), the density of coral colonies (excl. reef-building scleractinians), densities of individuals associating with coral habitats and mean richness (mean number of morphotypes per image) of associated fauna. Each dot represents a habitat segment. Lower matrix: correlation plots, upper matrix: Spearman coefficient and significance of the test (p-value: * ≤ 0.05 ; ** ≤ 0.01 , *** ≤ 0.001), diagonal data: distribution for each variable. (B) The relation between coral diversity based on 16 individuals (ES₁₆; x-axis) and the diversity of the associated fauna, based on 28 individuals (ES₂₈; y-axis). The red dots represent the biogenic habitats, the green dots represent the coral habitats on hard substrate and the blue dots represent the soft sediment dominated habitats.

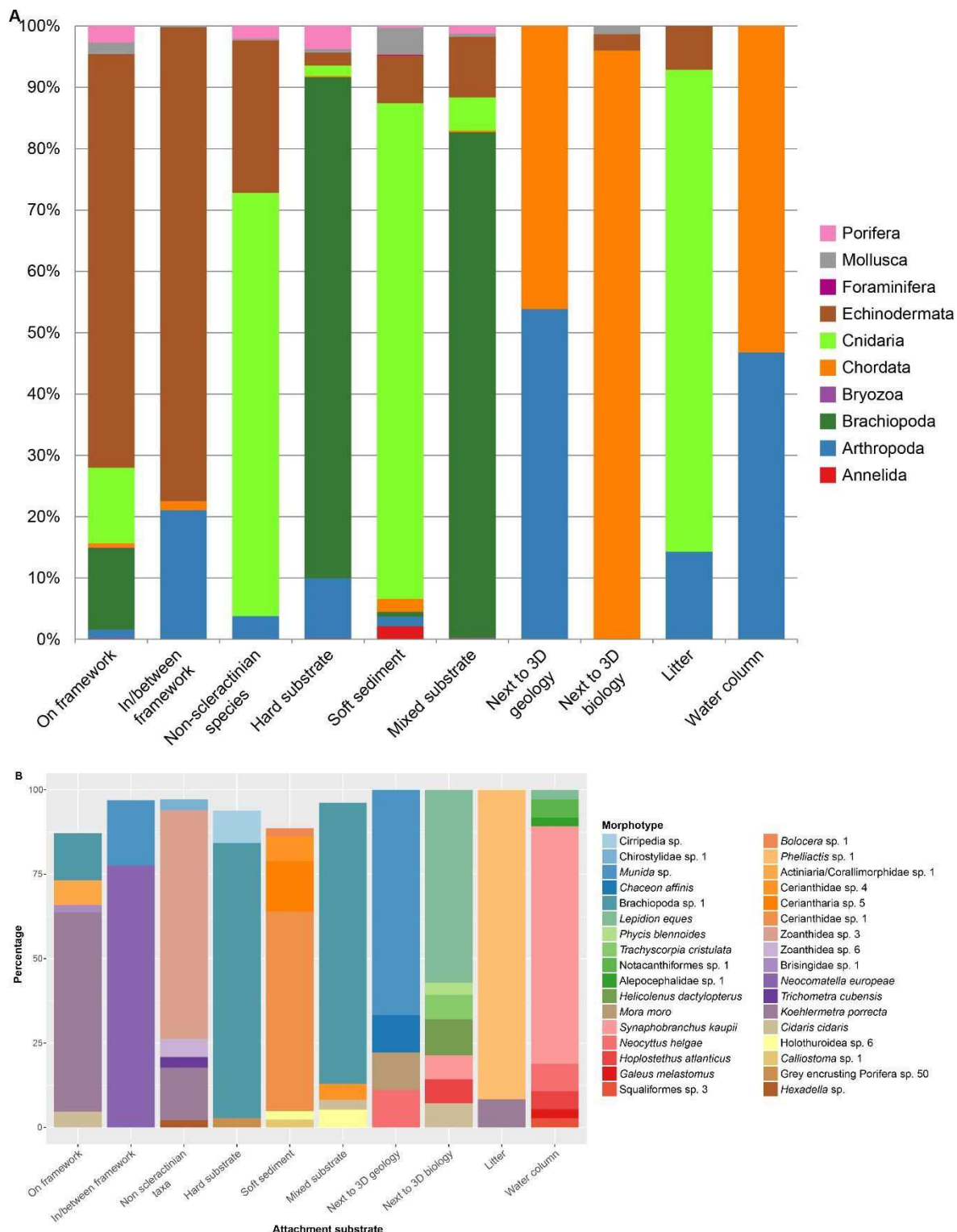
3.5. Attachments and feeding modes

The individuals associated with coral habitats were mostly suspension/filter-feeders, except in the solitary scleractinian on soft substrate habitat that is dominated by grazers (Fig 10). The proportion of suspension/filter-feeders is larger on biogenic and hard substrate coral habitats ranging from 81.7% to 97.2% than on soft substrate habitats, where contributions ranged from 41.0% to 73.5%. Grazers and predators/scavengers were more common on soft substrate habitats ranging from 2.9% to 49.2% and from 9.8% to 25.2%, respectively. The proportion of deposit feeders was low in all habitats.



Different types of substrates were colonised or dominated by different phyla (Fig 11A) and morphotypes (Fig 11B). The scleractinian framework was dominated by echinoderms. *K. porrecta* was the most common morphotype attached on the framework while another crinoid *Neocomatella europaea* was most common in/between the framework, similarly to the crustacean *Munida* sp. Non-scleractinian organisms, such as antipatharians and sponges, were mainly colonised by cnidarians. Zoanthidae sp. 3, contributing more than 60% to the composition, colonised the glass sponge *Aphrocallistes beatrix*, while Zoanthidae sp. 6 colonised antipatharians. The encrusting sponge *Hexadella* sp. colonized a *Geodia* sponge. *K. porrecta* as well as the crinoid *Trichometra cubensis* were also seen on gorgonians, such as *Narella vershuysi*. The litter was mainly colonised by the actinian *Phelliactis* sp. 1, but only few individuals were observed colonising litter items. Hard substrate and mixed substrate were colonised by mostly brachiopods. The cnidarians *Bolocera* sp. 1 (Actiniaria) and Cerianthidae sp. 1, sp. 4 and Ceriantharia sp. 5 were the main morphotypes attached to soft sediment. Chordata, represented largely by the fish morphotypes *Lepideon eques*, *Helicolenus dactylopterus*, *Mora moro* and *Neocyttus helgae*, were present especially next to 3-dimensional biological objects (excluding scleractinian framework), as well as next to 3-d geological objects. These 3-d geological ‘attachment’ possibilities was also used by arthropods, mainly

Munida sp. The fish *Synaphobranchus kaupii* was the Chordata contributing most to the individuals observed in the water column.



4. Discussion

This study gives new information about the megafaunal community structure and composition associated with a variety of coral habitats in submarine canyons of the Bay of Biscay. Over 32,500 individuals belonging to more than 160 morphotypes have been recorded in 10 different coral habitats. The general findings of this study are: (1) a high beta- and gamma-diversity characterise the faunal communities, and (2) the beta-diversity is according to substrate type. Previous studies have considered cold-water coral reefs formed by *L. pertusa* in the NE Atlantic as biodiversity hotspots (Jensen and Frederiksen, 1992; Roberts *et al.*, 2006; Rogers, 1999) favouring a denser and more diverse community than coral rubble or the surrounding soft sediment dominated habitats for macro- and megafauna (e.g. Buhl-Mortensen *et al.*, 2012; Costello *et al.*, 2005; Henry and Roberts, 2007; Mortensen *et al.*, 1995). The heterogeneity of coral reefs created by the complex three-dimensional structure of the framework can have an important role in enhancing this density and diversity (Buhl-Mortensen *et al.*, 2010; Mortensen *et al.*, 1995). With this knowledge, it was hypothesised that coral reefs in the submarine canyons of the Bay of Biscay would also support an abundant and diverse community of associated fauna. Further, it was hypothesized that the density and diversity of the community associated with cold-water coral habitats dominated by soft sediment would be low compared to biogenic or hard substrate habitats, as demonstrated by previous studies (Davies *et al.*, 2015; Mortensen *et al.*, 1995; Robert *et al.*, 2015). In addition, the cover of biogenic substrate, including live and dead framework and rubble of reef-building scleractinians, and the coral density was hypothesised to have a positive influence on the density and diversity of the associated megafaunal community.

4.1. Biogenic, hard and soft substrate coral habitats support heterogeneous associated megafaunal communities

Substrate type is a major factor influencing the community patterns of the associated fauna: (i) species composition is conformed to three main groups of habitats distinguished by their dominant substrate type, being biogenic, hard or soft substrate. Substrate type was also of importance to the corals constructing the habitats (Van den Beld *et al.*, 2017). Other studies have also shown the importance of substrate type, separating faunal compositions (off New Zealand: Bowden *et al.*, 2016; Hardangersfjord, Norway: Buhl-Mortensen and Buhl-Mortensen, 2014; Gully Canyon, Canada: Kenchington *et al.*, 2014; Rockall Bank, off Ireland: Robert *et al.*, 2014). Of course, species are usually specialized to colonise either hard substrate, including coral framework and rubble, or soft sediment.

In more detail, the habitats characterised by the three different substrate types differed in community structure. Hard substrate habitats were characterised by a high density and a low diversity of associated fauna, dominated by brachiopods. Biogenic habitats are characterised by an intermediate density and a high diversity of the associated fauna, although there is a dominance of *K. porrecta*. The communities on soft substrate habitats were characterised by low densities. This density is, however, underestimated. Compared to hard substrate where all the megafauna is visible on images, soft substrate provides a habitat where taxa can occur within

the sediment itself, and, thus, they are not visible on images. Many megafaunal organisms are known to bury themselves in sand or mud, e.g. the crustacean *Nephrops norvegicus*, bivalves and gastropods (Sardà, 1998). Even though some patterns and shapes of burrows could be allocated to certain species with the aid of the surroundings, e.g. *N. norvegicus* and the sea pen *Funiculina quadrangularis* share their habitats in Mediterranean canyons (Fabri *et al.*, 2014), it remains largely unknown what species is responsible for what type of burrow.

Besides low densities, the community on soft substrate habitats showed an equitability; a high diversity and no dominant morphotypes characterised these communities. This was surprising, considering that previous studies have found a low diversity on soft sediment dominated habitats (Davies *et al.*, 2015, Roberts *et al.*, 2015).

Considering the diversities of both the associated fauna and the corals constructing the habitats (see Van den Beld *et al.*, 2017), it appeared that the coral diversity and the associated fauna diversity correlated negatively with each other. While the associated faunal diversity was high on soft substrate habitats, the coral diversity was low. The opposite was the case for hard substrate habitats.

The different community structure and composition patterns seen in habitats dominated by the three substrate types can be explained by differences in competition or by niche differentiation.

4.2. Competition and niche differentiation may explain the influence of substrate type on community structure

Intra- and interspecific competition for resources, such as space and food, influences the structure and compositions of communities. However, until so far, studies to the importance of competition on deep-sea community is absent or rare (see McClain and Schlacher, 2015). Competition could cause a dominance of one or a few species in a habitat and therefore a less diverse community. The results of this present study indicate a high abundance of the sessile brachiopods in coral habitats on hard substrate and a high abundance of the mobile crinoid *K. porrecta* (can be considered as sessile while feeding) in biogenic habitats, especially in coral reefs, whereas a higher equitability exists on coral habitats on soft sediment. Both species may outcompete other species for space, food and/or other resources. On habitats dominated by hard substrate, space is the major limiting factor for sessile species and food and/or space for mobile species (Grant, 2000; Menge and Sutherland, 1976). In habitats on soft sediment, space is less limited, because of the three-dimensional characteristics of soft bottoms (Grant, 2000; Wilson, 1990). Individuals can bury themselves in the sediment, as described above, making the encounter rate between individuals of the same or different species lower (Wilson, 1990). This results in a lower intra- and interspecific competition on soft sediment dominated habitats and a more intense competition on habitats dominated by hard substrate or coral reefs (Grant, 2000). In this study, the densities of coral colonies and the cover of biogenic substrate had a limited influence on the structure of the associated fauna; a weak but significant, positive correlation was observed between these components. It may be possible that corals and the associated fauna make trade-offs between the high energy demanding interspecific competition and other processes, e.g. reproduction and growth. A higher density and diversity of the faunal community is possible, if the energy is allocated to other processes resulting in a lower

competition ability. However, the competition between the coral species forming the habitat and the associated taxa is rarely investigated, especially for megafauna. In Norwegian offshore and inshore reefs, the abundance of macrofaunal species was highest in boxcore samples with a live coral cover of more than 20%, but the species diversity was highest in samples with a proportion of live *L. pertusa* between 1 and 20% (Mortensen and Fosså, 2006). This may suggest that associated species compete with the live *L. pertusa* colonies, resulting in a community with a dominance of one or few species. A study in Whittard Canyon by Morris *et al.* (2013) suggested that octocorals may be outcompeted by live *L. pertusa* colonies, as the richness of octocorals was lower on cliffs covered by live scleractinians, than in areas further away from this *L. pertusa* habitat.

Species competition is generally thought to lead to species niche differentiation by either specialisation and/or an expansion of the niche (McClain and Schlacher, 2015). A minimal overlap of the niches of taxa reduces competition and allows taxa to co-exist in the same area (McClain and Schlacher, 2015). Sanders (1969) even hypothesised in his stability-time theory that the specialisation of species to narrow niches leads to a co-existence of species at competitive equilibrium, what could explain the equitability of soft sediment dominated habitats observed in this study. However, this equilibrium could only exist in stable environments (Sanders, 1969), while deep-sea environments do experience disturbances on temporal and regional scales (McClain and Schlacher, 2015).

Niche differentiation can occur by variations in bathymetrical ranges, in geographical ranges (Lumsden *et al.*, 2007), in food availability and uptake (Duineveld *et al.*, 2007; Iken *et al.*, 2001; Levin and Dayton, 2009), in flow (Levin and Dayton, 2009) and habitat type (Leverette and Metaxas, 2005). Niche differentiation can be a reason of the co-occurrence of many brachiopods in coral habitats on hard substrate, potentially suggesting that corals and sessile organisms of small sizes can live together. The co-occurrence of brachiopods and corals has also been observed in the Mediterranean Sea (off Sicily: Bo *et al.*, 2014; Santa Maria di Leuca Coral Province: Rosso *et al.*, 2010). These taxa probably have a different niche occupation. Despite both taxa are filter-feeders, the difference in size allows them to occupy a different part of the water column, and therefore, catching particles on different places. In this case, their niches are separated on a habitat level.

However, a niche separation on a trophic level may also cause brachiopods and corals to occur in the same area. The deep-sea brachiopod *Gryphus vitreus* feeds on fine particles or dissolved organic matter (Emig, 1989), while the coral *L. pertusa* is an opportunistic feeder, including zooplankton (Carlier *et al.*, 2009; Mueller *et al.*, 2014); similarly, the diet of *M. oculata*, *Desmophyllum dianthus*, *Leiopathes glaberrima* and *Paramuricea* sp. specimens collected at the Santa Maria di Leuca Coral Province (Mediterranean Sea) also includes zooplankton (Carlier *et al.*, 2009). Trophic niche differentiation has been observed for the pennatulacean species *Umbellula* sp., feeding on a higher trophic level than smaller pennatulacean species (Iken *et al.*, 2001), but the previous suggested habitat differentiation due to size differences may also contribute here. However, expansion of the trophic niche has also been observed in corals; *L. pertusa* enhanced the uptake of smaller particles in the presence of *Eunice norvegica* compared to the sizes it would have eaten without this symbiont polychaete (Mueller *et al.*, 2013). However, this shift is more likely an obligated shift, caused by the theft of large particles by *E. norvegica* from *L. pertusa* (Mueller *et al.*, 2013). It may be possible that gorgonians and

antipatharians switch on a different food source in the presence of other species feeding on the same food sources.

Niche partitioning can also lead to the co-occurrences of filter- and deposit feeders on soft sediment dominated habitats. Both feeding guilds have a different food source, i.e. particles suspended in the water column and particles deposited on the sediment, respectively. However, it is also argued that these two feeding guilds do compete for the limited particulate organic matter (Iken *et al.*, 2001).

Considering reef-building scleractinians, the microhabitats in coral reefs, i.e. the living framework, the dead framework, coral rubble, underlying soft sediments, the cavities in and the free spaces between the branches (Mortensen *et al.*, 1995; Roberts *et al.*, 2006) add to the niche differentiation of animals. These micro-niches, formed by the complex three-dimensional scleractinian framework, favour other organisms due to the variety of these niches (Roberts *et al.*, 2009).

Competition and/or niche differentiation at multiple levels may influence the community patterns of this study, where a high density and low diversity, dominated by a brachiopod species, characterised hard substrate habitats, an intermediate density and diversity characterised biogenic habitats and an equitability characterised soft substrate habitats. These underlying processes can also force the negative correlation between coral and associated species diversity. The three-dimensional structure of coral reefs creates many niches.

4.3. Functional role of the three-dimensional structure of reefs

In this study, densities of fauna associated with coral reefs were higher than those observed on the other habitats formed by colonial scleractinians (rubble, colonial scleractinians on hard or soft substratum). In terms of diversity, multiple patterns were observed: (i) the highest observed and expected total species richness were in reefs, (ii) the mean species richness was higher on reefs than on rubble, and (iii) a higher diversity was observed for both reef and rubble habitat than the other biogenic habitat in the form of colonial scleractinians on soft substrate. These community structure patterns suggest that the three-dimensional structure of reefs could enhance the density and diversity of the associated fauna, as suggested by other studies (Buhl-Mortensen *et al.*, 2010; Jensen and Frederiksen, 1992; Roberts *et al.*, 2006; Rogers, 1999). Coral reef provides resources to other organisms, creates a higher degree of habitat heterogeneity and provides refuges formed by the cavities within the framework.

4.3.1. The framework provides resources for other species

Resources provided by the framework of reef-building scleractinians include habitat and food. Filter-feeders benefit from an elevated position, as shown by the high abundances of *K. porrecta* seen on top of the scleractinian framework in this study. A higher position in the water column is equivalent to a better position in the current or in the benthic nepheloid layer (Buhl-Mortensen *et al.*, 2010) and an increase in food capture rates by filter-feeders. If *K. porrecta* was observed outside coral reefs, they were observed on ledges or rocky outcrops, probably for

similar reasons. Another crinoid *Trichometra cubensis* has been observed with the gorgonian *Narella versluysi* (Tyler and Zibrowius, 1992; this study).

The scleractinians forming the cold-water coral reefs also provides food and therefore predators and/or grazers occur on the scleractinian framework. In this study, many echinoids, including the species *C. cidaris*, were observed on the scleractinian framework. Fragments of both live and dead coral framework as well as mucus secreted by *L. pertusa* and *M. oculata* have been found in the guts of four echinoid species from *L. pertusa*/*M. oculata* reefs (Stevenson and Rocha, 2013), supporting the suggestion that *L. pertusa* and *M. oculata* can function as a food sources for echinoids and potentially gastropods (Rogers, 1999; Stevenson and Rocha, 2013; Vertino *et al.*, 2010; Wild *et al.*, 2008). The small organisms on the branches of *L. pertusa* and/or *M. oculata*, e.g. bacteria and foraminifera, form also important food sources for echinoids and gastropods (Jensen and Frederiksen, 1992; Rogers, 1999; Wild *et al.*, 2008). In addition, echinoids, e.g. *Araeosoma fenestratum* and *C. cidaris*, have been observed to feed on *K. porrecta* within coral reefs in the canyons of the Bay of Biscay (Stevenson *et al.*, 2017), supporting the presence of echinoids on scleractinian framework even more.

Coral reefs have a larger size and surface than coral rubble habitat or habitats formed by isolated colonies of reef-building scleractinians. Therefore, reefs could enhance the density and diversity in a greater extent than the other biogenic habitats, resulting into higher associated faunal densities and diversity as observed in this study. Other studies do support these observations: the diversity of Norwegian and Scottish coral reefs exceeded the diversity of areas covered by coral rubble for macrofaunal (Buhl-Mortensen *et al.*, 2012; Henry and Roberts, 2007; Mortensen and Fosså, 2006), megafaunal (Buhl-Mortensen *et al.*, 2012; Mortensen *et al.*, 1995), and fish communities (Costello *et al.*, 2005; Husebø *et al.*, 2002).

4.3.2. *Heterogeneity of hard and soft substrate in reefs*

Reef habitats in submarine canyons provide a high heterogeneity of both hard (including the framework) and soft substrate. The 71 morphotypes that were shared among the biogenic habitats and the other habitats dominating by hard or soft substrate is probably a result of this heterogeneity as it can change both diversity and species composition (Buhl-Mortensen *et al.*, 2012; Buhl-Mortensen and Buhl-Mortensen, 2014; Davies *et al.*, 2014; Kenchington *et al.*, 2014). Many coral reefs in submarine canyons are infilled with soft sediment, including those in the Bay of Biscay (De Mol *et al.*, 2011; Flögel *et al.*, 2014; Van den Beld *et al.*, 2017), due to a high sedimentation rate in canyons along with modified currents by the scleractinian framework (Mienis *et al.*, 2007) resulting in local sediment deposition. This allows the settlement of organisms specialised in either hard or soft substrate in the same area.

4.3.3. *The framework functions as a refuge against predation*

One of the functions suggested for coral reefs is to provide shelter for many organisms including commercially important fish species (Costello *et al.*, 2005; Mortensen *et al.*, 1995). Jensen and Frederiksen (1992) observed only juvenile organisms of many species associating with *L. pertusa* blocks on the Faroe shelf. The many cavities of the framework could be used by juveniles and smaller prey species, such as squat lobsters from the *Munida* genus, to hide from

predators. Indeed, *Munida* has been observed especially inside or between the framework (Buhl-Mortensen *et al.*, 2010; this study). Predator of this crustacean include the tusk *Brosme brosme* (Kutti *et al.*, 2015) that is often observed in high abundances between or around scleractinian framework on coral reefs (Costello *et al.*, 2005).

Due to the relation of prey species and scleractinian framework as well as other functions (not described here), it is suggested that *L. pertusa* (and *M. oculata*) reefs are important for fish species. Indeed, fish abundances were higher on *L. pertusa* (and *M. oculata*) reefs than areas outside the reefs along the European margin (Costello *et al.*, 2005; Husebø *et al.*, 2002; Linley *et al.*, 2016). More precisely, in a study including several locations off Norway, off Sweden, at Rockall Trough and Bank, at Porcupine Bank and Seabight and on a shipwreck in the Faroe-Shetland Channel, 92% of the observed fish species and 80% of the observed individuals were associated with reefs and/or rubble fields near the reefs (Costello *et al.*, 2005). *B. brosme* and *Conger conger* (conger eels) were more often observed on reefs than on non-reef areas off Norway, in the Rockall-Hatton Bank basin, Porcupine Seabight as well as in canyons of the Bay of Biscay (Biber *et al.*, 2014; Costello *et al.*, 2005; Linley *et al.*, 2016).

However, this association of fish with reefs is suggested to be species and/or region dependent (Auster, 2007; Biber *et al.*, 2014; Linley *et al.*, 2016) and, therefore, not always observed for total fish abundances (Biber *et al.*, 2014). In this study, no large aggregations were observed at the coral reefs in the canyons of the Bay of Biscay. In addition, the contributions of fish to the community composition were higher on soft substrate dominated habitats than on coral reefs, especially caused by the northern cutthroat eel *Synaphobranchus kaupii*. In previous studies, *S. kaupii* was mainly observed in sediment dominated areas (Biber *et al.*, 2014; Costello *et al.*, 2005; Linley *et al.*, 2016). Macrourids were also often observed on soft sediment dominated substrate (pers. obs.), although the taxonomic resolution of this group of fish was too low to include in the analysis. In Kaikoura Canyon, New Zealand, macrourids were often observed to prey on fauna in or on soft sediment as indicated by their head-down positions (De Leo *et al.*, 2010).

5. Conclusion

In this study, we have investigated the faunal community associated with coral habitats in submarine canyons of the Bay of Biscay. The density and diversity of the fauna associated with biogenic habitats, including coral reefs, support the hypothesis that biogenic habitats indeed show a higher diversity than hard substrate coral habitats. However, the diversity of soft substrate dominated habitats, at least of the habitat composed by sea pens, is higher than the hard substrate habitats and similar or even higher than the biogenic habitats. This type of habitat should therefore not be neglected in conservation plans. However, further research, including an increase in sample size of soft sediment dominated coral habitats, is necessary to confirm the potentially high diversity on soft substrate habitats. The occurrences of macro- and meiofauna on the sediment and erected organisms as well as the fauna in the sediment (including megafauna) needs to be investigated to give a complete view of the faunal communities in coral habitats.

Community patterns can partly be explained by substrate type and the underlying processes of competition and niche differentiation. The community of coral habitats on hard substrate and biogenic habitats were characterised by one dominant species, whereas there was more equitability and a higher species turnover on soft sediment dominated habitats. Stronger competition on hard substrate and biogenic habitats compared to the species competition on soft substrate habitats can explain this pattern. Competition may lead to niche differentiation, potentially explaining the co-occurrences of corals and associated fauna of small sizes on hard substrate habitats and of filter- and deposit-feeders on soft substrate coral habitats.

The complex three-dimensional structure of reef-building scleractinians, providing multiple micro-niches, may be important to enhance the density and diversity of associated fauna; both these measures were higher in reefs than in other reef-building scleractinian habitats with a smaller three-dimensional structure.

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Chapter 5

Marine litter in submarine canyons of the Bay of Biscay

Résumé français

Déchets marins dans les canyons sous-marins du Golfe de Gascogne

1. Introduction

La quantité, la distribution et la composition des déchets dans l'environnement profond ainsi que l'impact de déchets sur les communautés de faune abyssal sont encore mal connus (Galgani, 2015 ; Miyake *et al.*, 2011), malgré l'augmentation du nombre d'études sur ces problématiques (par exemple Galgani *et al.*, 2015 ; Pham *et al.*, 2014 ; Ramirez-Llodra *et al.*, 2013). Ces études ont montré qu'il y a une dominance des plastiques dans les canyons sous-marins ainsi qu'une présence de matériel de pêche (par exemple Galgani *et al.*, 2000 ; Mordecai *et al.*, 2011 ; Pham *et al.*, 2014 ; Ramirez-Llodra *et al.*, 2013 ; Schlining *et al.*, 2013 ; Tubau *et al.*, 2015).

Les canyons sous-marins, qui incisent les marges continentales, pourraient canaliser les déchets marins du plateau continental vers la plaine abyssale ou les canyons pourraient fonctionner comme un puits retenant les déchets de l'environnement profond (Mordecai *et al.*, 2011 ; Pham *et al.*, 2014 ; Schlining *et al.*, 2013).

Les canyons sous-marins du Golfe de Gascogne accueillent des habitats coralliens (par exemple De Mol *et al.*, 2011 ; Huvenne *et al.*, 2011 ; Reveillaud *et al.*, 2008) considérés comme vulnérables, menacés ou en déclin (FAO, OSPAR). Pour comprendre l'impact de déchets sur les habitats coralliens, il est nécessaire de déterminer quels types de déchets sont présents dans l'environnement profond et quelle est leur distribution.

Les canyons sous-marins du Golfe de Gascogne ont été explorés par une caméra tractée et un *Remotely Operated Vehicle* (ROV) pour répondre aux objectifs suivants : (i) déterminer la nature et les densités de déchets, (ii) établir les sources principales de déchets marins, (iii) évaluer l'influence des facteurs environnementaux sur la distribution des déchets marins dans et entre canyons, et (iv) explorer l'impact des déchets sur les communautés benthiques.

2. Matériels et méthodes

Quinze canyons sous-marins et trois sites sur l'interfluve ou le haut de la pente contigu aux canyons adjacents ont été explorés pendant trois campagnes, BobGeo en 2009, BobGeo 2 en 2010 et BobEco en 2011. Des images ont été acquises par les caméras verticales d'un système tracté pendant les deux premières campagnes et d'un ROV pendant BobEco. Des images ont été extraites des vidéos du ROV pour permettre une comparaison de ces images avec les photos prises par la caméra tractée.

Chaque image a été associée à une valeur de profondeur extraite de la bathymétrie et a subi un contrôle de la qualité (éclairage, netteté, distance au fond).

Les images répondant aux critères du contrôle qualité a été analysée pour (i) les déchets marins, (ii) la faune qui colonisent les déchets, et (iii) les structures géologiques et biogéniques. Les déchets ont été classés dans six catégories : « Plastiques », « Matériels de pêche », « Câbles et cordes », « Bouteilles en verre », « Autres déchets » ou « Déchets indéterminés ». Les structures du fond marin ont été identifiées et classées dans 4 catégories : « Coraux d'eau froide », « Autres structures biologiques », « Structures géologiques » et « Substrat nu ». Les densités de déchets ont été quantifiées et normalisées par 100 images. Pour chaque canyon nous avons calculé la proportion que représente chaque catégorie de déchet selon le nombre total de déchets observés. Le pourcentage d'images sur lesquelles figuraient des déchets a été calculé par classe de 300 m de profondeur et par catégorie de structure du fond marin.

3. Résultats

Au total, 198 déchets ont été observés sur 6255 images à l'échelle du Golfe de Gascogne, avec une moyenne de 3,2 objets par 100 images. Ils ont été observés pendant 25 des 29 plongées (86%) et dans les 15 canyons sous-marins ainsi que les 3 sites d'interfluve ou haut de pente contigu au plateau explorés pendant cette étude.

Les plastiques étaient dominants, représentant 42% des déchets observés (Fig. 2). La catégorie « matériel de pêche », comme des filets et palangres, était la deuxième catégorie la plus fréquente et représentait 16% des déchets observés (Fig. 2).

La distribution des types des déchets variait à l'échelle du Golfe de Gascogne (Fig. 3) : (i) les plastiques ont été principalement observés dans le centre et le sud du Golfe de Gascogne, (ii) les matériels de pêche ont été observés partout dans le Golfe de Gascogne, et (iii) les bouteilles en verre ont été observées principalement dans les canyons de la côte sud-ouest de la Bretagne. Deux sites d'accumulation de déchets ont été observés dans le Canyon d'Arcachon.

Les pourcentages d'images qui montrent des déchets, étaient plus élevés dans les classes de profondeur « 801–1100 m » et « 1401–1700 m » et les densités de déchets étaient significativement différents entre les classes de profondeur ($\chi^2 = 34,5382$; $df = 5$, $p \leq 0,001$) (Fig. 4).

La distribution de déchets par catégories de structure du fond marin était différente d'une distribution aléatoire ($\chi^2 = 44,363$, $df = 3$, $p \leq 0,0001$) (Table 4). La fréquence relative et la densité des déchets étaient plus élevées dans les zones avec des structures géologiques (4,3%, 9,9 déchets par 100 images), que les zones avec un relief biologique (coraux : 3,9%, 4,5 déchets par 100 images ; autres structures biologiques : 1,5%, 1,4 objets de déchets par 100 images) ou le substrat nu (1,3%, 1,5 déchets par 100 images) (Table 4).

Une différence significative a été observée entre les compositions de déchets associés aux types différents de structures du fond marin ($\chi^2 = 22,3062$, $df = 10$, $p = 0,01$) (Fig. 5). Cette différence était due à : (i) les bouteilles en verre étaient plus abondantes dans les zones où le relief était construit par des structures biologiques et absentes des zones avec une structure géologique, et (ii) la densité relative des plastiques était plus faible sur le substrat nu que les zones structurées par du relief biogénique ou géologique. Cependant, les matériels de pêche étaient répartis de façon uniforme sur les catégories de structures du fond marin.

Vingt-sept déchets (13.6% du total des objets de déchets observés) ont été colonisés, principalement par des suspensivores, comme des anémones, les scléactiniaires *Lophelia pertusa* et *Madrepora oculata*, des hydrozoaires, des éponges, les vers annélides de la famille des Serpulidae, des huîtres et des comatules. Les crustacés du genre *Munida* ont utilisé des plastiques et du tissu comme refuge. Des poissons ont été observés dans ou à proximité d'un grand filet de pêche.

4. Discussion

La majorité des déchets présents dans les canyons du Golfe de Gascogne, à l'exception des plastiques, proviendrait probablement des activités maritimes telles que la pêche, le transport maritime et la plaisance. Les bouteilles en verre ont été observées dans les canyons qui sont proches d'une voie de navigation majeure et les matériels de pêche ont été observés dans tout le Golfe de Gascogne, en cohérence avec la distribution de la pêche dans ce bassin (Lorance et Leonardi, 2011). Les activités maritimes pourraient être une source de plastiques également, mais il est peu probable que ce genre de déchets provienne uniquement d'activités maritimes ; beaucoup de plastiques pourraient être transportés de la terre à la mer par les rivières (Galgani *et al.*, 2000 ; Mordecai *et al.*, 2011 ; Ramirez-Llodra *et al.*, 2013).

Plusieurs facteurs environnementaux, comme les courants et la géomorphologie, pourraient avoir une influence sur l'accumulation de déchets. Les canyons sous-marins sont probablement des conduits pour le transport des déchets, particulièrement les plastiques légers (Galgani *et al.*, 2000 ; Galgani *et al.*, 1996 ; Mordecai *et al.*, 2011 ; Ramirez-Llodra *et al.*, 2011 ; Schlining *et al.*, 2013). Cette hypothèse est confirmée par la prédominance de plastiques observés dans 9 des 15 canyons incluent dans cette étude et est cohérente avec des observations dans des canyons sous-marins faites par d'autres études (Mordecai *et al.*, 2011 ; Tubau *et al.*, 2015). Le lien entre la profondeur et la densité de déchets n'est pas claire : elle peut être significativement positive (Galgani *et al.*, 2000 ; Schlining *et al.*, 2013 ; Tubau *et al.*, 2015), ou non significative (Fabri *et al.*, 2014 ; Mordecai *et al.*, 2011 ; Ramirez-Llodra *et al.*, 2013). Dans les canyons du Golfe de Gascogne, les densités de déchets variaient et les densités les plus élevées observées dans les classes de profondeur médianes (« 801–1100 m » et « 1401–1700 m »). Les variations d'abondance des déchets en fonction de la profondeur pourraient être causées par l'hydrodynamisme. Dans le Canyon de Cap-Ferret, par exemple, les sédiments s'accumulent à des profondeurs comprises entre 500 et 1500 m (Mulder *et al.*, 2012). Les structures géologiques et biologiques, qui augmentent la rugosité, pourraient également avoir une influence sur la distribution des déchets. Les déchets ont été trouvés piégés par ces structures dans certaines (Bergmann et Klages, 2012 ; Schlining *et al.*, 2013 ; Watters *et al.*, 2010). Dans cette étude, l'abondance relative des plastiques étaient plus élevée dans les habitats complexes que dans sur le substrat nu.

Les principaux impacts liés aux déchets marins sont l'étouffement, l'ingestion, l'enchevêtrement, la pêche fantôme et des dommages physiques à la faune fixe (Kühn *et al.*,

2015 ; Ramirez-Llodra *et al.*, 2011). Dans le Golfe de Gascogne, les habitats vulnérables, comme les habitats coralliens, se révèlent être des zones d'accumulation de déchets marins, particulièrement les plastiques, donc les déchets pourraient avoir un impact négatif sur les habitats vulnérables. Les déchets marins peuvent également fournir un nouvel habitat favorisant localement la diversité.

Les impacts cumulés des déchets marins et des autres pressions anthropiques, comme l'abrasion par des chaluts et le changement climatique, sont mal compris, mais il est nécessaire de mettre en place des mesures de protection et de prévention efficaces pour limiter l'entrée de déchets dans les océans.

5. Conclusion

L'étude de la densité et de la distribution des déchets dans ou à proximité de 15 canyons du golfe de Gascogne montre que ceux-ci sont présents dans tout le Golfe et atteignent des densités parmi les plus élevées observées sur les marges continentales Européenne dans l'Atlantique Nord-est jusqu'à 59.000 déchets par km².

Les déchets dans le Golfe de Gascogne ont des origines terrestres et maritimes. Les plastiques sont les plus abondants, représentant 42% des déchets observés, suivi par les matériels de pêche (16%).

La distribution des déchets est le résultat de l'interaction entre les sources de déchets, leur flottabilité et les échelles imbriquées des processus hydrodynamiques. Certains plastiques légers sont probablement arrivés par la Loire et la Gironde. Ces déchets sont probablement transportés par les courants jusqu'aux rebords du plateau continental puis le long de la pente. Dans les canyons, les courants de marée transportent les déchets légers plus profondément, jusqu'à ce qu'ils soient piégés dans des zones de dépôt, incluant des structures biologiques et géologiques complexes. Les coraux d'eau froide en particulier favorisent l'accumulation des plastiques. Les bouteilles en verre sont plus probablement liées aux activités maritimes, tandis que les matériels de pêche étaient distribués de façon homogène dans et entre des canyons.

Les matériels de pêche n'étaient pas préférentiellement associés aux coraux d'eau froide, mais, néanmoins, ils représentent 15 à 20% des déchets dans ces habitats. Bien que les déchets puissent fournir un habitat ou refuge pour des espèces benthique, les impacts cumulatifs de déchets et d'autres menaces anthropiques, comme la pêche et les changements climatiques, suggèrent que les mesures effectives de prévention devraient être mises en œuvre pour limiter les déchets dans l'environnement marin.

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Marine litter in submarine canyons of the Bay of Biscay

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ABSTRACT

Marine litter is a matter of increasing concern worldwide, from shallow seas to the open ocean and from beaches to the deep-seafloor. Indeed, the deep sea may be the ultimate repository of a large proportion of litter in the ocean.

We used footage acquired with a Remotely Operated Vehicle (ROV) and a towed camera to investigate the distribution and composition of litter in the submarine canyons of the Bay of Biscay. This bay contains many submarine canyons housing Vulnerable Marine Ecosystems (VMEs) such as scleractinian coral habitats. VMEs are considered to be important for fish and they increase the local biodiversity. The objectives of the study were to investigate and discuss: (i) litter density, (ii) the principal sources of litter, (iii) the influence of environmental factors on the distribution of litter, and (iv) the impact of litter on benthic communities.

Litter was found in all 15 canyons and at three sites on the edge of the continental shelf/canyon, in 25 of 29 dives. The Belle-  le and Arcachon Canyons contained the largest amounts of litter, up to 12.6 and 9.5 items per 100 images respectively. Plastic items were the most abundant (42%), followed by fishing-related items (16%). The litter had both a maritime and a terrestrial origin. The main sources could be linked to fishing activities, major shipping lanes and river discharges. Litter appeared to accumulate at water depths of 801–1100 m and 1401–1700 m. In the deeper of these two depth ranges, litter accumulated on a geologically structured area, accounting for its high frequency at this depth. A larger number of images taken in areas of coral in the shallower of these two depth ranges may account for the high frequency of litter detection at this depth. A larger number of litter items, including plastic objects in particular, were observed on geological structures and in coral areas than on areas of bare substratum. The distribution of fishing-related items was similar for the various types of relief. Litter items were mostly colonised by scleractinian corals and hydroids. Several fish species and a lithodid crab seemed to associate with the accumulated litter.

This extensive study showed litter to be widely distributed in the submarine canyons of the Bay of Biscay. These findings increase our understanding of the distribution of litter, its composition and accumulation and its impact on benthic communities.

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1. Introduction

The impact of human activities on the deep-sea environment has increased over recent decades, and this trend is predicted to continue in the near future (Ramirez-Llodra et al., 2011). The exploitation of living, mineral and energy resources are of particular concern, but there is also a growing body of evidence that litter is common and widespread, even in the deepest parts of the ocean (Miyake et al., 2011).

Litter on beaches and items floating on the surface of the ocean have been extensively studied (Galgani et al., 2015; Ryan, 2015). The interaction of this debris – especially plastics – with turtles, sea birds and marine mammals, through suffocation, ingestion and entanglement has been widely described in the literature (K  hn et al., 2015; Ryan, 2015). By contrast, little is known about the amount, distribution and composition of litter in the deep-sea environment, and its impact on deep-water habitats and benthic communities (Galgani et al., 2015; Miyake et al., 2011), although increasing numbers of studies are being undertaken to explore these issues (e.g. Galgani et al., 2015; Pham et al., 2014; Ramirez-Llodra et al., 2013). The studies carried out to date have indicated that plastic items predominate, at least in the Bay of Biscay

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(Galgani et al., 2000; Pham et al., 2014), four Portuguese canyons (Mordecai et al., 2011), several parts in the Mediterranean (Ramirez-Llodra et al., 2013; Tubau et al., 2015), the Gulf of Mexico (Wei et al., 2012), and along the shelf and slope of the west coast of the US (Keller et al., 2010), particularly in the Monterey Canyon (Schluning et al., 2013). Plastic longlines, originating from the fishing industry, were the main type of litter observed in the Azores (Pham et al., 2013) and off the coast of California (Watters et al., 2010), whereas ropes and gill nets were the most frequently observed items on the coral mounds off the Irish coast (Grehan et al., 2005). Fishing gear also dominated the litter found on the seamounts of Goringe Bank (NE Atlantic; Vieira et al., 2015), the Tyrrhenian Sea in the Mediterranean (Angiolillo et al., 2015) and off the coast of South-East Africa (Woodall et al., 2015).

Submarine canyons along continental margins may act as a conduit for the transport of marine litter from shallower to deeper waters, or as a sink, retaining the litter in the deep sea (Mordecai et al., 2011; Pham et al., 2014; Schluning et al., 2013). Based on submersible video surveys in the Bay of Biscay, Galgani et al., (2000) reported higher densities of marine litter at bathyal depths in submarine canyons than on the continental shelf.

There are about 135 submarine canyons along the continental margin of the Bay of Biscay (Bourillet et al., 2006). These canyons host many Vulnerable Marine Ecosystems (VMEs) constructed by corals, sponges and oysters (De Mol et al., 2011; Huvenne et al., 2011; Reveillaud et al., 2008; Van Rooij et al., 2010). VMEs are considered to be functional and biodiversity 'hotspots', providing structural complex habitats that locally enhance the diversity and biomass of benthic communities (Buhl-Mortensen et al., 2010). Cold-water coral reefs, in particular, are thought to be important for many fish species (Costello et al., 2005; Roberts et al., 2006), as they provide shelter, feeding sites, spawning grounds (Auster, 2007; Sulak et al., 2007), and nursery areas (Baillon et al., 2012). However, the species responsible for the construction of these VMEs may, like geological structures (e.g. boulders and rocky outcrops; Schluning et al., 2013; Watters et al., 2010), trap litter (Bergmann and Klages, 2012; Galgani et al., 2000).

The principal human activities in the Bay of Biscay are fishing and shipping. The French and Spanish fishing fleets operate in this area, with the French (deep-sea) fleet targeting grenadiers (Macrouridae spp., especially *Coryphaenoides rupestris*), black scabbard fish (*Aphanopus carbo*), monkfish (*Lophius* spp.) and langoustines (*Nephrops norvegicus*) in particular (ICES, 2015). This part of the Atlantic Ocean also hosts a number of commercial and recreational shipping lanes. Human activities can have major detrimental effects on VMEs, which are fragile and easily disturbed, and recover only slowly, if at all (Althaus et al., 2009; Williams et al., 2010).

There is a need to determine what types of litter are present and their distribution, if we are to understand their impact on VMEs. We used footage acquired with an ROV and a towed camera system between 2009 and 2011 to estimate the amount of litter, its composition and distribution within the canyon systems of the French part of the Bay of Biscay in the North-East Atlantic Ocean. The objectives of this study were: (i) to determine the density of litter, (ii) to establish the principal sources of litter, (iii) to consider the influence of environmental factors on the distribution of litter within and between canyons, and (iv) to investigate the impact of litter on benthic communities.

2. Material and methods

2.1. Study site

The Bay of Biscay is part of the North-East Atlantic Ocean located to the west of France and the north of Spain. It includes the Armorican and Aquitaine margins, which we studied here, and it is bounded by the Celtic margin in the north, and the North Iberian margin in the south. The Armorican margin extends from the Berthois Spur to the Conti Spur, with a broad continental shelf (up to 200 km) and a steep, canyon-dominated slope. By contrast, the Aquitaine margin extends from the Conti Spur to the Capbreton Canyon, and has a narrow shelf (70 km) and a smooth slope (Bourillet et al., 2006).

2.2. Data collection

Data were collected during two cruises on the R/V *Pourquoi Pas?* (Ifremer, France) – BobGeo in 2009 (Bourillet, 2009) and BobEco in 2011 (Arnaud-Haond, 2011) – and one cruise on the R/V *Le Suroît* (Ifremer, France) – BobGeo 2 in 2010 (Bourillet, 2010). The main objectives of these cruises were to study VMEs and/or geological features in canyons of the Bay of Biscay. Fifteen canyons were included in this study, mainly along the Armorican margin with the exception of the Arcachon Canyon located on the Aquitaine margin. In total, 29 dives were undertaken, 26 of which took place within canyons. The remaining three dives took place on the edge of the continental shelf/canyon (Table 1).

The Scampi towed camera system was used to collect data during 17 dives, and the Victor 6000 ROV during 12 dives (Table 1). The Scampi is equipped with a Nikon D700 photo camera directed vertically downwards. The system was towed at a mean speed of 0.9 knots, about 2–3 m above the seafloor. Photographs were taken at intervals of 10 to 90 seconds.

The Victor 6000 has multiple cameras. For the purpose of this study, we used the downward-facing video camera (Sony FCB-H11). For comparison of the footage obtained with the ROV and the images taken by the towed camera, frame-grabs were taken from the video footage at one-minute intervals, with ADELIE annotation software. These frame-grabs were analysed in the same way as the photographs obtained with the towed camera system. Hereafter, we use the term 'images' to refer to both frame-grabs from the ROV and photographs from the Scampi. We obtained a mean of 5.8 images 100 m^{-1} with the ROV (after averaging over all dives), and 5.3 images 100 m^{-1} with Scampi.

Metadata (image name, time code and latitude/longitude) were recorded with ADELIE software, for both the towed camera and the ROV.

A depth value was extracted for each image from Digital Terrain Models, with grid sizes of 15, 25 or 125 m (Bourillet et al., 2012). These depth values were used to calculate the mean, minimum and maximum water depth of each dive. The mean depth of the dives was between 228 and 1598 m (Table 1), with a minimum water depth of 223 m and a maximum water depth of 2359 m.

2.3. Data analysis

Images were subjected to quality control to ensure that litter items were reliably identified and counted. Two criteria were used for quality control: (i) altitude; images were excluded if they were taken less than 1 m or more than 5 m above the seafloor, and (ii) image quality; images were excluded if poorly focused, taken in low-light conditions or with a high particle load.

Each image was annotated for three sets of criteria: (i) marine litter, (ii) the fauna colonising the marine litter, and (iii) seafloor structures. Litter items were identified and allocated to one of six

Table 1

The number of litter, litter densities and main characteristics of the dive surveyed with the towed camera Scampi (BobGeo and BobGeo 2) or the ROV Victor 6000 (BobEco). The names of the canyons are listed from north to south. Litter densities per canyon are given in bold; it consists of the results of one dive if there was only one dive performed in that specific canyon or it consists of the mean between several dives when multiple were undertaken in one canyon. Standard deviations are provided between brackets, if possible. Mean values for the Bay of Biscay are also provided.

Canyon	Cruise	Dive	Av. Depth (m)	Min. depth (m)	Max. depth (m)	Length (km)	Tot no. Images	No. litter items	No. items per 100 image
Sorlingues	BobEco	477	746.6	381.4	1240.5	9.21	588	3	0.5
Sorlingues	BobEco	472	1598.2	1095.6	2358.6	2.94	180	0	0
Sorlingues (mean)						6.07 (± 4.43)	384 (± 288)	1.5 (± 2.1)	0.4
Petite Sole	BobEco	471	794.8	657.7	1000.4	7.86	458	6	1.3
Petite Sole	BobEco	476	955.0	943.0	964.9	2.63	199	3	1.5
Petite Sole (mean)						5.25 (± 3.70)	329 (± 183)	4.5 (± 2.1)	1.4
Lampaul	BobEco	478	805.2	509.1	1249.9	11.13	516	8	1.6
Shelf-N	BobGeo	1	291.5	223.4	353.9	2.05	97	2	2.1
Chapelle	BobGeo	3	467.1	426.9	527.4	0.80	20	0	0
Chapelle	BobGeo	4	784.8	560.3	1062.2	1.61	100	1	1.0
Chapelle	BobGeo	2	621.9	404.0	1082.0	2.93	150	2	1.3
Chapelle (mean)						1.78 (± 1.08)	90 (± 66)	1.0 (± 1.0)	1.1
Crozon	BobEco	479	929.9	673.9	1385.7	10.07	492	12	2.4
Morgat	BobGeo	5	742.4	418.3	1205.4	4.00	280	29	10.4
Morgat	BobGeo	6	707.8	572.9	915.8	1.06	81	3	3.7
Morgat (mean)						2.53 (± 2.08)	181 (± 141)	16 (± 18.4)	8.9
Morgat - Douarnenez	BobEco	480	880.9	704.6	1201.3	8.50	388	14	3.6
Guilvinec	BobEco	469	877.0	790.5	923.9	4.71	303	15	5.0
Odét	BobGeo 2	6	700.9	345.2	1172.3	6.66	352	9	2.6
Odét	BobGeo	10	722.0	625.5	897.4	1.48	86	0	0
Odét	BobGeo	7	880.9	645.9	1320.9	2.83	213	7	3.3
Odét	BobGeo	9	710.1	542.9	917.6	2.15	140	1	0.7
Odét (mean)						3.28 (± 2.32)	198 (± 115)	4.3 (± 4.4)	2.1
Shelf-S	BobGeo 2	5	228.4	227.1	229.1	0.99	56	2	3.6
Shelf-S	BobGeo	8	334.8	293.4	393.3	2.71	173	11	6.4
Shelf-S (mean)						1.85 (± 1.22)	115 (± 83)	6.5 (± 6.4)	5.7
Belle-île	BobGeo	11	681.5	418.8	987.8	2.09	143	18	12.6
Croisic	BobEco	468	836.1	711.9	940.3	2.97	197	1	0.5
St. Nazaire	BobEco	467	1495.5	1148.1	1763.2	2.15	129	5	3.9
Rochebonne	BobEco	465	949.8	587.2	1498.6	3.25	134	5	3.7
Ars	BobEco	466	801.8	517.1	1094.7	2.90	172	1	0.6
Ars	BobGeo 2	1	717.6	463.3	1196.5	5.16	207	2	1.0
Ars (mean)						4.03 (± 1.59)	190 (± 25)	1.5 (± 0.7)	0.8
Arcachon	BobGeo 2	2	1261.4	1103.6	1534.4	5.21	151	0	0.0
Arcachon	BobGeo 2	3	1392.9	1261.4	1517.1	4.35	76	30	39.5
Arcachon	BobGeo 2	4	933.6	768.9	1086.8	4.52	174	8	4.6
Arcachon (mean)						4.69 (± 0.46)	134 (± 51)	12.7 (± 15.5)	9.5
Bay of Biscay			836.4	223.4	2358.6	119 (total)	6255 (total)	198 (total)	3.2 (mean)

Table 2

Details about the items allocated to each category 'Plastics', 'Fishing-related items', 'Cables and ropes' and 'Other items'. The category 'Glass bottles' does not need to be detailed, since only glass bottles are allocated to this category. The items in 'Unidentified items' are not specified neither, since it was impossible to identify these items. Individual items are in alphabetical order.

Plastic	Fishing-related items	Cables and ropes	Other items
Bags	Gill- or trawl nets	Cables	Artillery
Fake Christmas tree	Longlines	Ropes	Ceramic cups
Hard plastics	Mesh	Wires	Ceramic plates
Sheets	Parts of fishing gear		Cloth/fabrics
Tubes	Traps		Metal drinking cans
			Metal items
			Metal pipe
			Rubber tubes

categories: 'Plastic', 'Fishing-related items', 'Cables and ropes', 'Glass bottles', 'Other items' and 'Unidentified items' (Table 2). The category 'Fishing-related items' included only items that could confidently be linked specifically to fishing activities. The fishing fleet may also discard plastic items, glass bottles or cables and ropes, but it is not possible to affirm a particular origin for these categories. Thus, we assigned non-specific plastic items, such as plastic bags and sheets to the 'Plastic' category, longlines to

'Fishing-related items' and rubber and metal products to 'Other items' (Table 2). If a particular item was visible on more than one image, it was counted only once, to prevent duplication and ensure a conservative estimate.

The presence or absence of colonising fauna was recorded. The colonising fauna was identified to the lowest possible taxonomic level. Mobile species, such as ophiuroids and crinoids, were recorded as colonising fauna only if they were found in or on the litter. Highly mobile species, such as fish and large crustaceans, were recorded interacting with litter items if the distance between the species and the item did not exceed about two body lengths.

The seafloor structure criterion was used to investigate the influence of the local relief on the distribution of litter. Seafloor relief may result from the construction of biological structures such as corals, sponges and xenophyophores, or geological structures, such as pebbles, cobbles and rocky outcrops (Table 3). Four categories were defined: "Corals", "Other biological structures", "Geological structures" and "Bare substratum".

Litter densities were quantified and normalised per 100 images. The contribution of each type of litter to the total number of items encountered during a complete dive was calculated as a percentage. In most cases, only one dive was performed per canyon. If multiple dives were performed within the same canyon, the numbers of items attributed to each category were averaged between dives before the calculation of percentages. We included

Table 3

The different biological and geological structures constructing each relief-category.

Coral	Other biological species	Geological structures	Bare sediment
Antipatharians	Actinaria	Boulders	Consolidated mud
Gorgonians	Brachiopoda	Cobbles	Gravel
Scleractinians	Cerianthids	Pebbles	Hard substrate
Scleractinian rubble	Oysters	Mix of two or more of the above	Soft sediment
Seapens	Oyster and other shell debris	Rocky outcrops	
Mix of two or more of the above	Sponges	Ledges	
Mix of corals and xenophyophores	Xenophyophores	Steps	
		Very high slope	
		Walls	

multiple dives for a given canyon if the dives took place far enough apart to ensure that they did not cross paths and none of the items would be counted twice.

The presence or absence of litter on each image was also used to investigate the difference in litter densities with water depth. The percentage of images showing litter was calculated from the total number of images for each 300-m depth class. These depth classes were chosen to optimise the trade-off between the number of classes, the class interval and the number of observations in each class in the depth range of our dataset (water depth of ~200–2400 m). Seven depth classes were chosen of which two depth classes were merged into a single class, because they contained too few images for separate analysis (> 1701 m depth), resulting in six classes in total. A chi-squared test was used to assess the influence of water depth.

The density of litter in each seafloor structure category was normalised on the basis of the total number of images in the corresponding category and is expressed in litter items per 100 images. The percentage of images showing litter was calculated from the number of images showing at least one item of litter and the total number of images in each category. A chi-squared test was used to assess differences in litter abundance between categories on the basis of presence/absence data for each image.

3. Results

3.1. Distribution and composition of litter

In total, 198 individual litter items were recorded on the 6255 images analysed (Table 1). We observed a mean of 3.2 items per 100 images over the entire Bay of Biscay. However, the distribution and densities of items differed considerably between dives and between canyons. Litter items were observed in 25 of the 29 dives (86%). Litter was found in all 15 canyons and in the three dives located at the edge of the continental shelf/canyon. However, no litter was found in four single dives (Sorlingues Canyon, BobEco, dive 472; Chapelle Canyon, BobGeo, dive 3; Odet Canyon, BobGeo, dive 10; and Arcachon Canyon, BobGeo 2, dive 2). The maximum number of litter items detected in a particular dive was 30, equivalent to 39.5 items per 100 images, for the Arcachon Canyon (BobGeo 2, dive 3). However, litter density was highest in the Belle-île Canyon (12.6 items per 100 images; BobGeo, dive 11) if we averaged the findings for the three dives in the Arcachon Canyon. The second highest mean density of litter was that for Arcachon Canyon, at 9.5 items per 100 images (BobGeo, dives 2, 3 and 4). The third highest mean density of litter was that of Morgat Canyon (8.9 items per 100 images; BobGeo, dives 5 and 6).

Overall, 42% of the items observed were made of plastic, mostly bags or sheets (Figs. 1A and 2). Fishing-related items, such as nets and longlines (Fig. 1C) were the second most frequent category of items found, accounting for 16.2% of all the litter items observed

(Fig. 2). “Cables and ropes” (Fig. 1B) accounted for 6.1% of litter items. “Glass bottles” (Fig. 1D), “Other items” and “Unidentified items” accounted for 8.6%, 15.2% and 11.6% of litter items, respectively (Fig. 2). The “Other items” category included an artillery shell, ceramics and metallic items (Fig. 1E).

The distributions of the various types of litter differed in the Bay of Biscay (Fig. 3). Plastic items were observed mostly in the central and southern parts of the Bay of Biscay. Fishing-related items and cables and ropes were found all over the Bay of Biscay, but their relative abundance was highest in Ars Canyon (66.7% of all litter items found in this canyon). Glass bottles were observed predominantly in the canyons off the coast of southwest Brittany, with the highest percentages obtained for the interfluvial between the Douarnenez and Morgat Canyons (35.7%), and for Crozon Canyon (25.0%). The highest percentages for “Other items” were obtained in the centre of the Bay of Biscay (Douarnenez-Morgat: 35.7%; southern-most location on the shelf near Odet Canyon: 30.8%).

Two sites of litter accumulation were identified in Arcachon Canyon: (i) a fishing net trapping at least 20 pieces of plastic and (ii) a longline, plastic items, cloth and an item resembling a piece of glass.

3.2. Depth classes

The percentages of images showing litter items were highest for the ‘801–1100 m’ and ‘1401–1700 m’ depth classes, at 3.2% and 7.4%, respectively (Fig. 4). The percentages of images showing litter items were less than 2% for all other depth classes. Litter density differed significantly between depth classes ($\chi^2=34.5382$; $df=5$, $p<0.001$). We initially thought that this difference might be the result of litter accumulation at two sites within Arcachon Canyon, both in the 1401–1700 m depth class. However, this difference remained significant after the removal of these accumulations from the analysis ($\chi^2=17.9053$; $df=5$, $p=0.003$).

3.3. Influence of seafloor structures

The relief created by geological or biological structures influenced the distribution of litter (Table 4). The observed distribution of litter between seafloor structure categories was significantly different from a random distribution ($\chi^2=44.363$, $df=3$, $p<0.0001$). The relative frequency and density of litter were higher in areas with elevated geological structures (4.3%, 9.9 items per 100 images), than in areas with other types of relief (corals: 3.9%, 4.5 items per 100 images; other biological species: 1.5%, 1.4 items per 100 images) or bare substratum (1.3%, 1.5 items per 100 images).

The accumulations in the Arcachon Canyon mentioned above were located next to rocky outcrops, which largely accounted for the influence of geological structures. When these accumulations were removed from the analysis, the number of images showing

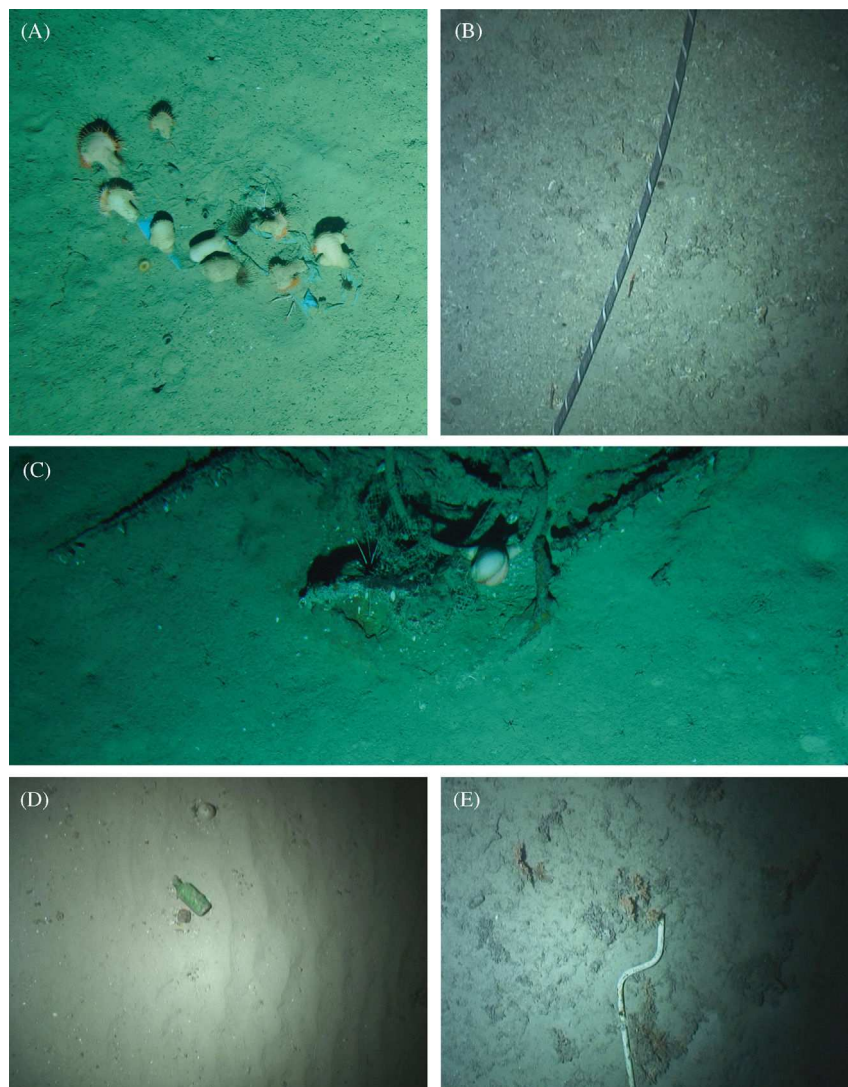


Fig. 1. Examples of marine litter; each representing one of six categories: (A) “Plastic items” (BobGeo 2 cruise); (B) “Cables and ropes” (BobEco cruise); (C) “Fishing-related items” (BobGeo 2 cruise); (D) “Glass bottles” (BobEco cruise) and (E) “Other items” (BobEco cruise).

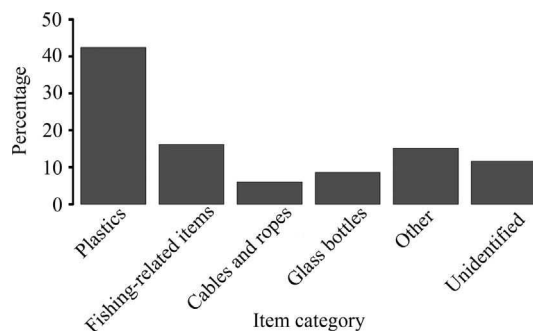


Fig. 2. The proportion items corresponding to each category in the Bay of Biscay (205 items in total).

litter decreased to 11, leading to decreases in average litter density to 3.4 items per 100 image and the percentage of images showing litter to 2.5% (based on 435 images from the “geological structures” category). However, even with the elimination of these accumulations, the influence of seabed structure on litter distribution remained significant ($\chi^2=39.3524$, $df=3$, $p < 0.0001$).

The number of items allocated to the different litter categories differed between seafloor structures (Fig. 5). There were too few

litter items in areas in which the relief was constructed by organisms other than corals for valid chi-squared tests. We therefore merged this category with the ‘corals’ category. The composition of the litter associated with the three remaining types of seafloor structure (biological structures, geological structures and bare substratum), differed significantly from a random distribution ($\chi^2=22.3062$, $df=10$, $p=0.01$).

This difference was driven by differences in the relative abundance of glass bottles, plastic and other items. Glass bottles were absent from areas of geological structure and were more abundant in areas in which the relief was constructed by biological organisms. The relative density of plastic items was lower on bare substratum than on biologically or geologically structured areas. “Other items” were observed predominantly on bare substratum.

By contrast, fishing-related items were more evenly distributed, with percentages of 41% for biological structures, 59% for geological structures and 29% for bare substratum.

The distribution of seafloor structures differed between the depth classes described above (Fig. 6). The relative abundance of seafloor structures formed by corals was higher in the ‘801–1100 m’ and ‘> 1701 m’ water depth classes ($\chi^2=1147.897$, $df=15$, $p < 0.0001$). Interestingly, the accumulations observed at depths of 1401 to 1700 m in the Arcachon Canyon were located in an area in

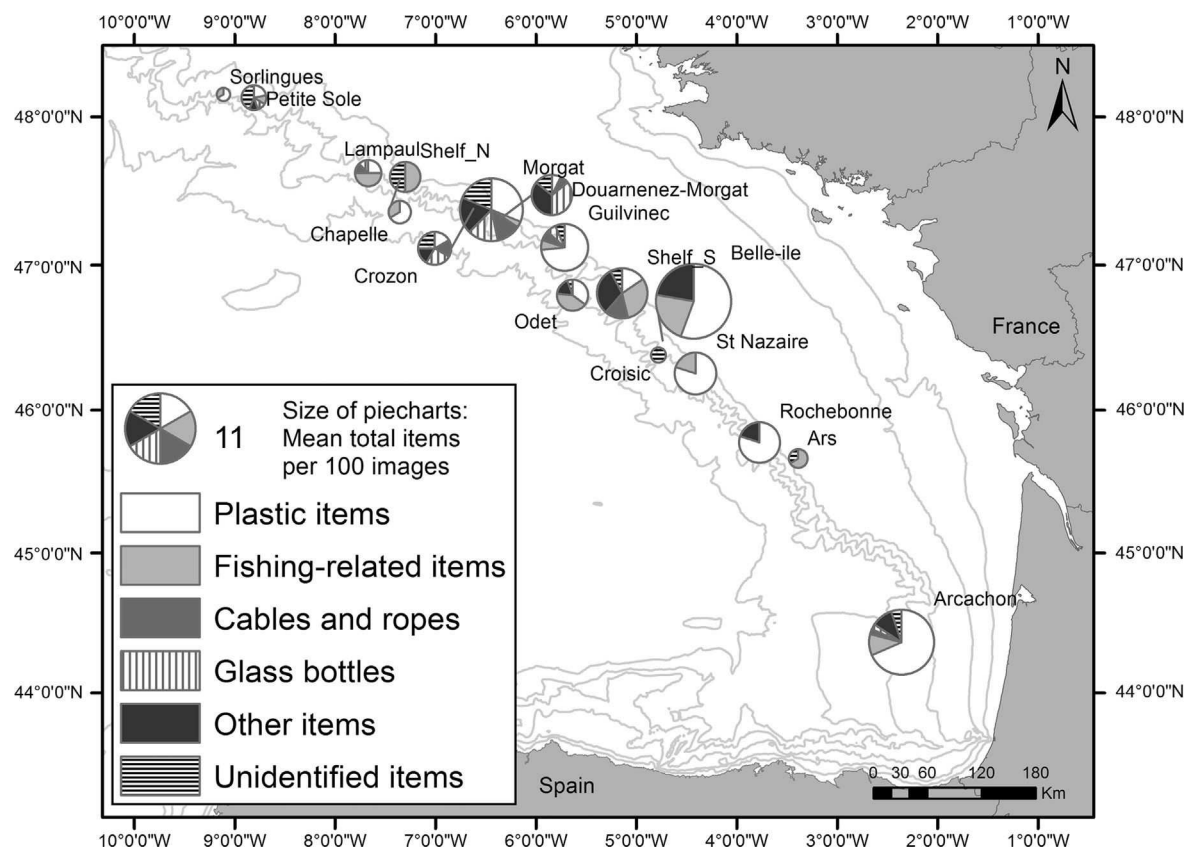


Fig. 3. The distribution and composition of litter in the canyons of the Bay of Biscay. The pie charts represent the proportion of each litter category among the total items found in the canyon concerned.

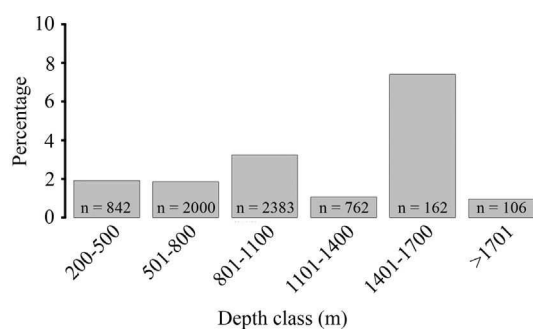


Fig. 4. The percentages of images showing signs of litter, from the total number (*n*) of images per 300-m depth class.

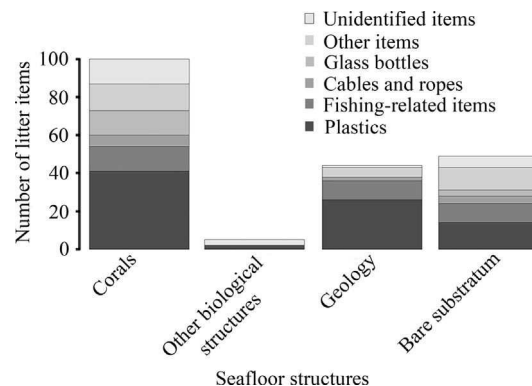


Fig. 5. The number of items allocated to each litter category within the different seafloor structures.

Table 4

The litter densities, percentages of images showing one or more items of litter and the total number of images for each relief-areas: "Corals", "other biological species", "geological features" and "bare substratum".

Relief-type	Total number of images	Number of images showing litter	Litter density (items 100 per images)	Percentage images showing litter
Coral	2216	85	4.5	3.9
Other biological species	345	5	1.4	1.5
Geological structures	443	19	9.9	4.3
Bare substratum	3251	42	1.5	1.3

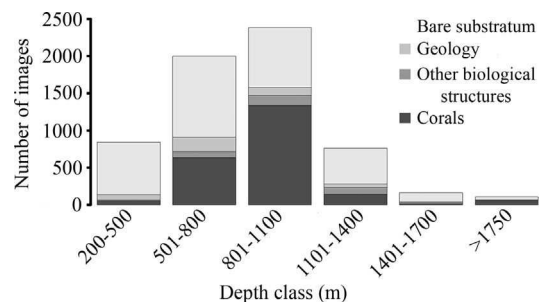


Fig. 6. The distribution of seafloor structures within each depth class.

which the relief is formed by geological structures, even though geological structures were rare in this depth class.

3.4. Colonising fauna

Twenty-seven items (13.6% of the items observed) were colonised, mostly by sessile suspension feeders. Plastic items, fishing gear, ropes and cloth were colonised by actinians (at least three different species; e.g. see Fig. 1A). Scleractinians (*Madrepora oculata*, *Lophelia pertusa* and/or solitary corals) and hydroids generally colonised fishing gear, such as longlines, nets and traps, and cables. One cable was also found to be encrusted with sponges and serpulids. The artillery shell was colonised by oysters. Mobile species, such as crinoids and ophiuroids were observed on plastic materials, fishing gear and cables. Single occurrences of a holothurian next to a part of a trawl net, the echinoid *Cidaris cidaris* in a fishing net and an unidentified echinoid (probably *Echinus* spp.) on a cable were also recorded. Crustaceans of the genus *Munida* were found to use plastic items and cloth as burrows. About 12 fish (Macrouridae spp., *Synaphobranchus kaupii* and *Lepidion eques*) and a lithodid crab were found close to a large fishing net and longlines. Another seven fish were found further away, but still less than five body lengths from the item. However, it was difficult to determine whether the fish in or very close to the net were still alive.

Sixty-four items (32.3%) were either partly buried or covered by a very thin layer of sediment.

4. Discussion

4.1. Litter density in the Bay of Biscay

Marine litter is one of the qualitative descriptors for which goals have been set for the achievement of Good Environmental Status in the European Marine Strategy Framework, and it is one that needs to be tackled urgently (Galgani et al., 2013). Knowledge about the amounts, nature and origin of litter at the European scale is essential for the definition of priority areas and management strategies. However, it is often difficult to compare the results of different studies, due to the use of diverse methods for data acquisition and analysis. Trawling surveys can sample buried litter and small items but integrate litter distribution data over large distances which prevents precise localisation of each litter item recovered in the net. On the other hand, optical surveys can provide a precise geolocalisation of items as well as additional information about the local environmental and the biological setting, but only for visible macroscopic litter. In both cases, quantification of the area sampled or observed is an issue. For optical surveys, an estimation of the absolute size of an image requires lasers or precise information about the position and attitude of the vehicle (altitude, pitch, roll) and the camera (pan, tilt, zoom). In this study, we used cameras directed vertically downwards. This approach should, theoretically, provide more accurate estimates of absolute image size than approaches using a forward-directed camera. Unfortunately, the available information about the attitude of the Scampi was not precise enough for the accurate quantification of image size. In addition, the design and processing of optical surveys may complicate comparisons even further. Several studies have analysed still images (this study; Bergmann and Klages, 2012; Mordecai et al., 2011; Pham et al., 2014), whereas other have analysed a continuous video (Pham et al., 2013, 2014) or a combination of still and video images (Fabri et al., 2014). Image-based surveys, with non-contiguous images, provide a sub-sample of video surveys that does not capture the full range of the heterogeneity of litter distribution.

Aware that our optical, image-based surveys were likely to underestimate litter density, we still asked whether our results were in the same range as reported in previous studies, or more than an order of magnitude different. Based on the calibration of the ROV camera and the mean altitude of ROV dives (2.5 m above the seafloor), we estimated that the area of seafloor observed in each image was 6.6 m². This value was used to extrapolate litter densities from the number of items per 100 images to the number of items km⁻².

In the Bay of Biscay, the mean litter density was 4813 items km⁻² and the litter density per dive ranged from 0 to 9626 items km⁻². Outliers of 15,643 (Morgat Canyon), 18,952 (Belle-île Canyon) and 59,412 (Arcachon Canyon) items km⁻² were observed. Mean litter density in the canyons of the Bay of Biscay was an order of magnitude higher than the highest densities reported from trawling on the continental shelf (Galgani et al., 1995), confirming that canyons along continental margins act as a sink for marine litter (Pham et al., 2014). The range and mean densities of litter in our study were consistent with previous observations in canyons of the NE Atlantic and the Mediterranean Sea (Pham et al., 2014). The outlier values of density obtained for the Belle-île and Arcachon Canyons, 200 km and 75 km from land, respectively, were, however, unusually high, well above those reported for the Lisbon Canyon (6600 items km⁻², 27 km from land, Mordecai et al., 2011), and higher than, but not dissimilar to those reported for the La Fonera Canyon (15,057 items km⁻², 4 km from land, Tubau et al., 2015), thus establishing a new record for European canyons. The densities calculated here are also higher than those already reported for similar and nearby canyons in the Bay of Biscay. Pham et al. (2014) reported a litter density in Guilvinec Canyon two times lower than the one given in this study (3190 vs. 7521 items km⁻²) and a litter density for Whittard Canyon only one third of that obtained for the nearby Sorlingues Canyon in our study (140 vs. 602 items km⁻²). These discrepancies may indicate the existence of methodological biases in these comparisons, which should be considered with caution. However, this study, like others, highlights considerable spatial heterogeneity in the distribution of litter, possibly reflecting the variability of and distance from sources, the shape and activity of the canyons and the roughness of the seafloor (Galgani et al., 2000; Mordecai et al., 2011; Tubau et al., 2015; Woodall et al., 2015).

4.2. Influence of human activities on the nature and distribution of litter

Litter on the deep-sea bottom may be of terrestrial or maritime origin. Terrestrial sources probably predominate for plastics, which, due to their buoyancy, can travel large distances before settling down on the seafloor (Bergmann and Klages, 2012; Pham et al., 2014). Mordecai et al. (2011) concluded that most of the litter in Lisbon Canyon probably came from the land, because this canyon is located close to the shore. Litter from the land can be transported into the sea by rivers, and thence to the canyon system. This process clearly occurs at the submarine extension of the Rhone into the Gulf of Lion in the Mediterranean Sea (Galgani et al., 2000), the discharges of the Tordera River into the western Mediterranean (Ramirez-Llodra et al., 2013; Tubau et al., 2015) and the Gironde estuary in the Bay of Biscay (Galgani et al., 1995). The predominance of plastic items among the litter observed in this and other studies (Galgani et al., 2000; Mordecai et al., 2011; Pham et al., 2014; Ramirez-Llodra et al., 2013; Schlining et al., 2013; Tubau et al., 2015) may indicate a major input of litter from terrestrial sources, but it is difficult to determine their precise source (Pham et al., 2014). The highest mean densities of plastics were observed in the Belle-île and Arcachon Canyons. The continental shelf is at its widest in the region of the Belle-île Canyon, but this

section of the Armorican margin is probably under the influence of the Loire River (Jouanneau et al., 1999) and has a high abundance of litter (Galgani et al., 2000). The Arcachon Canyon may be affected by discharges from the Gironde estuary, which are directed to the south west (Jouanneau et al., 1999), because zones of litter accumulation are found in this direction but at some distance from the estuary (Galgani et al., 2000). The coastline facing the Belle-île and Arcachon Canyons also attracts large numbers of tourists and recreational sailors, potentially contributing significantly to the accumulation of plastic items in these two canyons.

Litter of maritime origin is more easily traced because it consists of rapidly sinking debris, such as glass bottles (Ramirez-Llodra et al., 2013), and activity-specific material such as pieces of longlines, nets and traps from the fishing industry. The number of glass bottles observed was highest for the Crozon Canyon and for the adjacent canyons and interfluvies to the south (the Morgat and Douarnenez Canyons). This area is crossed by a major shipping lane, extending from the west of Spain to the English Channel. Many of these glass bottles may have been discarded from ships, because the disposal of glass at sea is still permitted beyond the territorial waters of states (> 12 nautical miles from the nearest land; Annex V of the Convention for the Prevention of the Pollution from Ships MARPOL 73/78). Another major shipping lane in the Bay of Biscay crosses the canyon system near the Croisic and Belle-île Canyons. No glass bottles were observed in these canyons, but we cannot exclude the possibility that litter discarded from ships also contributed to the large amount of plastic items found in Belle-île Canyon.

Fishing activities are widespread throughout the Bay of Biscay (Lorance and Leonardi, 2011), and this is reflected in the observed distribution of fishing-related items. Fishing-related items were observed in 11 canyons and on the edges of the continental shelf near the Lampaul and Odet Canyons.

Most litter items, with the exception of plastic items, present in the canyons of the Bay of Biscay therefore probably originated from the maritime activities of the fishing, commercial and recreational sectors. These activities may also be a source of plastic items, but such items are unlikely to be of purely maritime origin, with many such items being transported from the land to the sea via rivers.

4.3. Influence of environmental factors on litter distribution

Marine litter is not distributed evenly over the deep-seafloor (Pham et al., 2014; Ramirez-Llodra et al., 2013). Environmental factors may modify the transport and permanent deposition of litter. These factors include currents, which interact with topographic features at various spatial scales and are a major driver of the distribution of litter (Galgani et al., 2000; Mordecai et al., 2011). Canyons, which funnel deep-water currents from the shelf to the abyss, have been identified as large topographic features likely to act as a conduit for litter transport, particularly for light plastics (Galgani et al., 2000, 1996; Mordecai et al., 2011; Ramirez-Llodra et al., 2011; Schlining et al., 2013). This hypothesis is confirmed by the predominance of plastic items among the litter observed in nine of the 15 canyons included in this study, consistent with the findings of other canyon-related studies (Mordecai et al., 2011; Tubau et al., 2015). Pham et al. (2014) found that litter densities were higher in submarine canyons than in other physiographic settings, such as continental shelves and seamounts, banks and mounds. The composition of litter in a submarine canyons is different compared to other settings. Half the items of litter found in submarine canyons were made of plastic (Pham et al., 2014), whereas only a small percentage of plastics were observed on seamounts (Pham et al., 2014; Vieira et al., 2015).

Within canyons, litter transport and accumulation vary with the natural dynamics of the canyon and the roughness of the seafloor (Schluning et al., 2013). As canyons are thought to act as conduits of both natural and anthropogenic materials, litter might be expected to accumulate towards the lower parts of canyons. However, analyses of the depth distribution of litter have not given consistent results between canyons. Some studies have reported an accumulation of litter at greater depths (Galgani et al., 2000; Schluning et al., 2013; Tubau et al., 2015), but others have reported an absence of a relationship between depth and litter distribution (Fabri et al., 2014; Mordecai et al., 2011; Ramirez-Llodra et al., 2013). Downslope accumulations of litter have been suggested in canyons actively carrying sediment towards the deep-sea fan (Galgani et al., 2000; Mordecai et al., 2011). Stronger dense shelf water cascading events may also explain the transport to and accumulation of litter at greater depths in the Cap Creus Canyon than in La Fonera Canyon, in the Western Mediterranean Sea (Tubau et al., 2015). In the canyons of the Bay of Biscay, litter density varied according to depth. Litter was most abundant in the middle depth classes ('801–1100 m' and '1401–1700 m') in our study. However, little is known about current dynamics in the canyons of the Bay of Biscay. Along the Armorican margin, current strength and direction are driven by internal tides, and net downslope currents have been recorded in the upper parts of the Guilvinec, Audierne and Blackmud Canyons, with instantaneous current speeds as high as 1 m s^{-1} (Khrifounoff et al., 2014; Mulder et al., 2012). Net down-canyon currents extend to depths of 1500 m in the Audierne Canyon, whereas up-canyon currents predominate at this depth in the Blackmud Canyon. In both canyons, an alternation of up- and downslope currents suggests that particles should be trapped in these canyons (Mulder et al., 2012). This and the roughness of the seafloor (see below) may account for litter being most abundant in the middle of the depth range. Canyon dynamics may be different along the Aquitaine margin. In the Cap Ferret Canyon, just north of the Arcachon Canyon, the upper part of the canyon above 500 m depth, is a by-passing area, with sediments, and probably litter, passing straight through to accumulate in the middle region, at depths of 500 to 1500 m (Schmidt et al., 2014). The Arcachon Canyon has a distinctive morphology, more like a channel-levee system, with a broader canyon thalweg and very gentle flanks (De Chambure et al., 2013). Areas of deposition towards the lower part of the Arcachon Canyon may account for the accumulation of large amounts of litter, resulting in high densities for the 1401–1700 m depth class.

In addition to depth, complex biological and geological structures significantly influence the distribution of litter in the canyons of the Bay of Biscay. Indeed, geological features, such as ledges, sand dunes, terraces and boulder fields, and biological structures, such as corals, may trap litter and prevent its onward transport with the current (Galgani et al., 1996). More litter was seen in rocky areas than in sandy habitats or habitats with cobbles off California (Watters et al., 2010). In the Monterey Canyon, litter tended to accumulate in high-relief outcrops or in depressions (Schluning et al., 2013). Large numbers of *Cladorhiza gelida* sponges were frequently found entangled with plastic, due to their emerging characteristics (Bergmann and Klages, 2012). In the Bay of Biscay canyons, the relative abundance of plastics, which are thought to be particularly prone to transport by currents, was higher in complex habitats than on bare substratum. Moreover, these complex habitats were dominated by corals, particularly along the Armorican margin, where they occurred predominantly in the 801–1100 m depth class. In the lower part of the Arcachon Canyon, complex structures were rare, but the largest accumulations of litter in the 1401–1700 m depth class were nevertheless observed next to rocky outcrops. Seafloor roughness is thus a major driver of the local distribution of lighter marine litter, such

as plastic items, which are trapped equally efficiently by biologically and geologically complex habitats.

Several environmental factors, such as current (speed and direction) and geomorphology, can influence the accumulation of litter. These factors may act at different scales, from the entire Bay of Biscay down to individual canyons and, even small geological and biological structures.

4.4. Impact of litter on benthic communities

Litter can affect marine species and habitats by entanglement, suffocation, ghost fishing and/or physical damages to the sessile fauna (Kühn et al., 2015; Ramirez-Llodra et al., 2011). In the Bay of Biscay, VMEs, such as coral habitats, were found to be hotspots of litter accumulation, especially plastics. There was no evidence of a direct impact of plastic items on the benthic communities. However, fibres and particles released by plastic degradation may eventually be ingested by the suspension-feeders that are dominant in coral communities (Thompson et al., 2004). The effect of such contamination remains unclear, but it may have a cumulative effect with other anthropogenic factors (fishing, chemical contamination, climate change), resulting in a significant impact on deep-sea coral communities.

Fishing-related items were found throughout the Bay of Biscay and, unlike plastics, were not preferentially associated with corals or with any other complex habitat. This suggests that fishing-related items may be too heavy for displacement by currents. However, 15 to 20% of the marine litter found in corals (including cable and ropes) was related to fishing activities, highlighting this additional, potentially strong pressure on the health status of corals.

In addition to its negative impacts, marine litter may provide a new habitat locally favouring beta diversity. Litter was found to be colonised by marine species from various taxonomic orders in this study, as in others. For example, actinians were found to have colonised a plastic sheet (this study; Fig. 1A), serpulid worms have been found on a missile (Wei et al., 2012), hydroids have been observed on a metal oil drum (Mordecai et al., 2011) and the brachiopod *Grypheus vitreus* has been found on clinkers (Ramirez-Llodra et al., 2013). Litter items may provide protective structures for mobile fauna, fish in particular (Bergmann and Klages, 2012; Watters et al., 2010). In this present study, several fish (Macrouridae spp., *S. kaupii* and *L. eques*) and a lithodid crab species were seen in and around a large fishing net. The fish trapped in the net were probably dead, attracting the macrourids and *S. kaupii*, known to be scavengers (e.g. Cousins et al., 2013; Priede et al., 1990; and references therein). However, the net may also provide shelter, accounting for the presence of *L. eques*. Angiolillo et al. (2015) reported mobile species, such as crustaceans, echinoids and octopuses, using litter as a refuge, similar to *Munida* in our study.

It appeared that 13.6% of the observed litter items in the Bay of Biscay was colonised, which is much less than 80% of litter reported by Angiolillo et al. (2015) and 67% reported by Bergmann and Klages (2012), of which the latter did not distinguish between colonisation or other interactions, such as entanglement. However, interactions between fauna and litter are rarely quantified in the literature and therefore the extent of litter colonisation or association remains largely unknown. The effects of such associations on the composition of benthic communities locally and regionally also remain to be determined. Such associations may increase local diversity, as seen in Portuguese canyons (Mordecai et al., 2011), but the replacement of existing species by other naturally occurring fauna can lead to non-natural changes to the composition of the local fauna (Bergmann and Klages, 2012), with effects on predation and competition for space and food. Colonisation may occur to such an extent that older litter items may eventually be

completely covered by organisms, such as the reef-building scleractinian corals that cover the artificial substrate provided by oil rigs in the North Sea (Bell and Smith, 1999; Gass and Roberts, 2006).

The effects of litter on benthic communities thus remain unclear, but the risk of cumulative adverse effects and application of the precautionary principle should foster an increase in public awareness and the establishment of regulations to prevent litter entering the oceans. Awareness of the presence of VMEs and the negative impact of human activities on those ecosystems is increasing. This awareness is the first step towards the establishment of measures limiting the introduction of litter into the submarine canyons of the Bay of Biscay. The establishment of Marine Protected Areas (MPAs), marine reserves and/or no-take zones (Ramirez-Llodra et al., 2011) is among the measures that could be taken. There is currently only one such zone in the Bay of Biscay, the no-take zone of Capbreton Canyon (Delayat and Legrand, 2011; Sanchez et al., 2013). A consensus between policy makers, scientists, industries making use of the deep-sea environment (e.g. fisheries and oil and gas companies) and all other relevant stakeholders could be developed for this and other measures, such as stricter regulations on the disposal of rubbish.

5. Conclusion

An analysis of litter density and distribution on image footage showed litter to be widespread in the Bay of Biscay, with some of the highest densities ever found on European continental margins in the North-East Atlantic (up to 59,000 items km⁻²). This extensive study involved 29 dives in 15 canyons and at three other sites on the edge of the continental shelf/canyon.

The litter in the Bay of Biscay is of both terrestrial and maritime origin. Plastic items were the most abundant type of litter, accounting for about 42% of the items observed, followed by fishing-related items (16%).

The distribution of litter resulted from the interplay between litter sources, litter buoyancy and the nested scales of hydrodynamic processes. Some of the lighter plastic items probably arrived in the canyons from the Loire and Gironde rivers. These items would have been transported by large-scale currents to the shelf break and downslope. Within canyons, internal tides transported the light litter further downslope, until it eventually became trapped in areas of deposition, including complex biological and geological structures. Corals were found to be particularly favourable structures for the accumulation of plastic items. Glass bottles seemed to be linked to shipping activities, whereas fishing-related items were more evenly distributed both within and between canyons.

Fishing-related items were not preferentially associated with corals, but they nevertheless accounted for 15–20% of the debris in these habitats. Even though litter has been shown to provide a habitat or shelter for benthic species, the cumulative impacts of litter and other anthropogenic pressures, such as fishing and climate change, suggest that effective prevention measures should be implemented to limit the discarding of litter in the marine environment.

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Conclusions and perspectives

Conclusions (version française)

Cette étude rapporte des nouveaux résultats sur la distribution et la diversité des habitats coralliens dans les canyons sous-marins du Golfe de Gascogne. Les objectifs principaux étaient de : (i) décrire l'hétérogénéité et la diversité des habitats coralliens aux différentes échelles spatiales, (ii) identifier les facteurs qui contrôlent cette distribution et les espèces structurantes à l'échelle régionale et l'échelle locale, (iii) décrire la structure des communautés de mégafaune associées à ces habitats coralliens et identifier les facteurs abiotiques et biotiques influençant la communauté, et (iv) décrire la nature et la distribution des déchets et évaluer leurs impacts potentiels sur les habitats coralliens.

Pour répondre à ces objectifs, 24 canyons et 3 sites sur des interfluves ou hauts de la pente contigus à 2 canyons ont été explorés pendant 46 plongées avec le ROV Victor ou la caméra tractée Scampi. Les images acquises au cours de ces plongées ont été annotées afin de déterminer l'habitat, les organismes coralliens et non-coralliens, la nature et le taux de couverture en substrat biogénique, dur et meuble ainsi que les déchets. L'influence des facteurs biotiques et abiotiques sur la distribution et la structure des habitats coralliens, des espèces coralliennes et leur faune associée a été étudiée.

Cette étude accroît les connaissances sur la distribution et la diversité des habitats coralliens à l'échelle du Golfe de Gascogne. Onze habitats coralliens définis d'après le système de classification du projet européen CoralFISH ont été observés et cartographiés. Un total de 62 morphotypes coralliens a été identifié, appartenant aux scléactiniaires, antipathaires, gorgones et pennatules, soulignant ainsi la grande diversité des coraux dans le Golfe de Gascogne. La communauté de faune associée aux habitats coralliens est également riche, totalisant 191 morphotypes, dont 160 morphotypes uniques.

Le substrat : un facteur déterminant la structure et la composition des assemblages de coraux et leurs faunes associées

Le type de substrat est un facteur structurant des assemblages de coraux et leurs faunes associées. Les espèces de coraux étant inféodées soit aux substrats durs soit aux substrats meubles, une nette dichotomie a été observée entre assemblages coralliens des habitats de substrat dur/biogénique et de substrat meuble.

Les habitats biogéniques et les habitats coralliens sur substrat dur partagent des compositions d'espèces similaires, à l'exception des scléactiniaires récifaux. *Lophelia pertusa* et *Madrepora oculata* créent localement de véritables récifs offrant un habitat biogénique tandis que surtout *Solenosmilia variabilis* forment des agrégations sur substrat dur. Les assemblages de coraux sur substrat meuble se caractérisent quant à eux par un *turnover* d'espèces élevé. Chaque habitat est en effet dominé soit par une pennatule, soit par une gorgone soit par un scléactiniaire solitaire et cette agrégation est quasi-monospécifique. Plusieurs hypothèses peuvent être émises pour expliquer cette ségrégation spatiale des espèces de coraux sur substrat meuble. Premièrement, la taille des grains ou la composition des sédiments pourraient être importants

pour les coraux qui colonisent les substrats meubles. En particulier, l'efficacité du système de fixation de ces coraux, un pédoncule chez les pennatules, un crampon chez les gorgones Isididae voire, l'absence de système de fixation chez certaines scléactiniaires solitaires pourrait être conditionnée par la composition et la compaction des sédiments. Deuxièmement, des interactions avec la mégafaune fouisseuse, par exemple la langoustine *Nephrops norvegicus*, causant des modifications de la structure de sédiment, pourraient avoir une influence sur le développement des coraux. Certaines pennatules, par exemple *Funiculina quadrangularis*, sont souvent observées dans des zones avec de terriers et la convention d'OSPAR a listé les « Colonies de pennatules et mégafaune fouisseuse » comme un habitat menacé et/ou en déclin. Cependant, l'interaction possible entre les pennatules et *N. norvegicus* est mal comprise. Troisièmement, différentes niches trophiques pour ces différents ordres et espèces de coraux pourraient également expliquer leur ségrégation spatiale sur substrats meubles. Le régime alimentaire des espèces coralliennes demeure largement inconnu et nécessiterait d'être précisé.

Conformément à notre hypothèse, la nature du substrat a également un rôle structurant sur les assemblages de faunes associées aux coraux. Trois groupes d'assemblages ont été observés : (i) les assemblages associés aux habitats biogéniques, dominés par la comatule *Koehlermetra porrecta*, (ii) les assemblages associés aux habitats coralliens sur substrat dur, dominés par des brachiopodes, et (iii) les assemblages associés aux habitats coralliens sur substrat meuble pour lesquels aucune espèce n'est dominante et l'équitabilité est élevée. Ces différents patrons entre substrats durs ou biogéniques et substrats meubles pourraient s'expliquer par des pressions de compétition variables. La compétition entre espèces est en effet généralement plus forte dans des habitats benthiques de substrat dur que des habitats de substrat meuble. Les habitats de substrat meuble ont une structure tridimensionnelle créée par la possibilité de s'enfouir dans le sédiment. Ceci réduit la compétition pour l'espace et la nourriture entre individus et, donc, limite la préemption d'une ressource par une ou peu d'espèces dominantes sur le substrat meuble. Une compétition interspécifique élevée pourrait également exister dans les habitats biogéniques, même si les habitats biogéniques ont une structure tridimensionnelle. La forte dominance de *K. porrecta* suggère en effet que cette comatule préempte les ressources spatiales et trophiques au détriment des autres espèces de filtreurs.

Les régimes hydrodynamique et sédimentaire déterminent la distribution des habitats coralliens aux échelles régionale et locale

La distribution des habitats coralliens est hétérogène à l'échelle du Golfe de Gascogne : dans le sud de la marge armoricaine et sur la marge aquitaine, les habitats coralliens sur substrat meuble dominant tandis que les habitats à scléactiniaires vivants sont absents. A l'échelle d'un canyon, la distribution des habitats est également hétérogène : les occurrences de scléactiniaires étaient plus élevées sur le flanc nord-ouest et les pennatules plus fréquentes sur le flanc sud-est. Les distributions aux deux échelles spatiales pourraient être expliquées par le type de substrat, résultant d'une interaction entre processus hydrodynamiques et sédimentaires : les forts courants érodent le fond marin en exposant le substrat dur, tandis que les courants plus faibles favorisent des taux de sédimentation élevés. A l'échelle du bassin, les canyons incisant la marge

Aquitaine ont une topographie plus lisse, caractéristique de taux de sédimentation élevés et de courants faibles favorisant les habitats coralliens sur substrat meuble. A l'échelle d'un canyon, le courant dominant dans le Golfe de Gascogne est orienté vers le nord et érode préférentiellement le flanc nord-ouest favorisant les scléactiniaires par rapport au flanc sud-est qui est plus sédimentaire et favorise les habitats coralliens sur substrat meuble.

L'influence des facteurs géographiques, géomorphologique et océanographiques : une question de la résolution ?

D'après la littérature, la profondeur, la latitude, la température, la salinité, le type de substrat ainsi que la pente et de la rugosité sont les principaux facteurs influençant la distribution des habitats coralliens et leurs espèces structurantes. Cette hypothèse ne peut être ici ni acceptée ni rejetée.

En association avec la nature du substrat, la pente a une influence sur la distribution des habitats coralliens. Les habitats à scléactiniaires vivants se développent préférentiellement dans les canyons et sur une pente de plus de 10° alors que les débris de coraux sont plus fréquents sur les pentes faibles des interfluves entre canyons ou du haut de pente contigu au plateau. L'influence de la pente est plus forte pour les habitats biogéniques et les habitats coralliens sur substrat dur que pour les habitats coralliens sur substrat meuble.

La profondeur, la latitude, la température, la salinité et des mesures de la rugosité sont peu discriminantes pour les habitats coralliens dans cette étude : les habitats coralliens présentent des conditions environnementales similaires aux résolutions auxquelles ces facteurs environnementaux sont disponibles. La résolution spatiale des facteurs environnementaux est plus faible que l'extension spatiale des habitats et pourrait limiter le pouvoir prédictif des modèles de distribution qui se basent classiquement sur ce type de données.

Les récifs de coraux et les habitats coralliens sur substrat meuble sont des *hotspots* de biodiversité

La comparaison des assemblages faunistiques des différents habitats coralliens a révélé les patrons suivants : (i) les densités de la faune associée aux récifs sont plus élevées que les densités de la faune associée aux autres habitats à scléactiniaires, (ii) la richesse spécifique moyenne par image des récifs de coraux est plus élevée que celle des débris de coraux, (iii) la diversité régionale des habitats biogéniques est plus élevée que celle des habitats coralliens sur substrat dur, (iv) les diversités locale et régionale des habitats coralliens sur substrat meuble sont similaires ou même plus élevées que la diversité des habitats coralliens sur substrat dur et des habitats biogéniques, et (v) la diversité des assemblages faunistiques est négativement corrélée à la diversité des coraux.

La densité élevée des récifs coralliens et la diversité régionale élevée des habitats biogéniques supportent l'hypothèse que les récifs de coraux sont des *hotspots* de biodiversité dans les canyons sous-marins du Golfe de Gascogne et qu'ils soutiendraient une communauté de faune associée à la fois dense et variée. La structure tridimensionnelle complexe des scléactiniaires

récifaux augmente l'hétérogénéité de l'habitat ce qui pourrait expliquer la diversité élevée des habitats biogéniques.

Étonnamment et contrairement aux hypothèses de départ, les habitats coralliens sur substrat meuble présentent une diversité locale et régionale élevées. De plus, les densités réelles et la diversité de ce type d'habitat sont probablement sous-estimées, puisque seulement l'épifaune a été observée sur les images. L'effort d'échantillonnage restant limité, il convient d'interpréter avec prudence les patrons de diversité observés sur les habitats coralliens sur substrat meuble. Les résultats de cette étude sont néanmoins prometteurs et soulignent que ces habitats nécessitent une attention particulière, tant d'un point de vue scientifique qu'en matière de gestion environnementale.

Les coraux d'eau froide sont menacés par les activités humaines

Cette étude donne une description de la distribution des déchets dans 15 canyons du Golfe de Gascogne. Les plastiques sont les plus abondants, suivies par les matériels liés à la pêche, par exemple des filets et des palangres. La distribution spatiale est hétérogène et pourrait être liée aux sources des déchets, à l'hydrodynamisme ainsi qu'aux patrons de sédimentation dans les canyons. Le relief du fond marin formé par des structures biologiques et géologiques, par exemple des colonies de coraux et des blocs rocheux, peut piéger les déchets, particulièrement les plastiques souples et a donc également une influence sur la distribution des déchets.

Les déchets marins pourraient impacter les coraux d'eau froide par étouffement, enchevêtrement ou ingestion. Les résultats de cette étude montrent que les déchets et les coraux d'eau froide pourraient être co-occurrent : (i) les déchets, en particulier les plastiques, s'accumulent dans des zones à relief, dû à la présence de colonies de coraux et des structures géologiques, et (ii) les déchets étaient plus abondants dans la gamme de profondeur où se concentre également de nombreux coraux. Ceci pourrait avoir des implications en termes de conservation, même si c'est un défi de quantifier l'impact des déchets sur les coraux.

Dans cette étude, un impact de la pêche est suggéré par les différences de distribution des récifs de coraux et des débris de coraux. Les récifs de coraux occupent préférentiellement des zones plus profondes et plus pentues dans les canyons, inaccessibles aux chaluts, tandis que les débris de coraux se situent majoritairement sur des zones plates des interfluves et du haut de la pente continentale, accessibles au chalutage. Ces observations supportent l'hypothèse que les canyons fonctionneraient comme des refuges naturels pour les coraux profonds.

Perspectives (version française)

Cette étude contribue significativement à une meilleure compréhension de la distribution des habitats coralliens d'eau froide dans le Golfe de Gascogne et leurs communautés associées. Cependant, quelques questions restent en suspens et d'autres émergent. Les déterminants environnementaux du développement des coraux d'eau froide restent à éclaircir pour être capable de comprendre ce qui distingue des récifs et jardins de coraux de colonies isolées. Plus largement, ces processus pourraient nous permettre de comprendre pourquoi certains récifs de coraux se développent jusqu'à former des monts carbonatés, tels ceux de la marge irlandaise, tandis que d'autres restent d'ampleur spatiale limitée et très majoritairement composés de colonies mortes, telle la majorité des récifs observés dans le golfe de Gascogne.

Effort et stratégie d'échantillonnage

Dans cette étude, comme dans la plupart des études dédiées aux coraux d'eau froide, l'effort d'échantillonnage parmi tous les habitats coralliens observés n'était pas équilibré. Plusieurs campagnes et plongées visaient spécifiquement des récifs et débris de coraux, donc l'échantillonnage est biaisé. L'effort d'échantillonnage sur les habitats coralliens sur substrat dur, en particulier ceux créés par des antipathaires ou gorgones, ainsi que les habitats sur substrat meuble est plus faible. L'acquisition de données supplémentaires sur ces habitats sous-échantillonnés contribuerait à une compréhension de leur distribution ainsi que de la structure et la composition de leurs assemblages. Cela permettrait de confirmer la diversité élevée de la faune associée aux habitats coralliens sur substrat meuble, qui était inattendue.

Des plongées supplémentaires pourraient être effectuées sur la marge Armoricaire méridionale et la marge Aquitaine où l'effort d'échantillonnage est également faible par rapport à la marge Celtique et le reste de la marge Armoricaire. Enfin, des plongées supplémentaires pourraient également être effectuées en deçà de 1500 m de profondeur.

La classification géomorphologique des canyons a permis d'identifier des structures telles que les bancs dans les canyons ou les terrasses sur les interfluvés pour lesquelles très peu de données ont été récoltées. Cette classification géomorphologique est le résultat d'interprétations d'experts qui a probablement une valeur prédictive plus élevée que les données de brutes de pente ou autres dérivés de la bathymétrie. A l'avenir, cette classification devrait guider les stratégies de plongées dans les canyons et ainsi aider à mieux comprendre les liens entre géomorphologie et distribution des coraux. *In fine*, préciser ce lien pourrait aider à la mise en place de stratégies de préservation des habitats coralliens dans des zones où il n'y a pas d'observations.

Une dernière stratégie d'échantillonnage pourrait se concentrer sur un canyon afin d'explorer la distribution et l'écologie des habitats coralliens à une échelle plus petite. Une telle stratégie est déjà mise en œuvre dans le canyon de Whittard, un canyon qui incise la marge Celtique, juste au nord de notre zone d'étude. Chacune des quatre branches de ce canyon sont étudiées de manière intégrée, incluant des observations de coraux par des ROVs, des mesures de courant, de flux de particules et d'hydrologie et de sédimentation grâce au mouillage de courantmètres, de CTD et de pièges à particules. C'est un défi de mesurer et comprendre l'hydrodynamisme et

la sédimentation dans les canyons sous-marins, parce que ce sont des processus complexes qui sont influencés par la topographie des canyons. Dans notre zone d'étude, le canyon de l'Odet, pour lequel l'effort d'échantillonnage est déjà important et dans lequel sept différents habitats coralliens ont été observés, pourrait être un bon candidat pour un tel programme d'échantillonnage et de cartographie à haute résolution spatiale.

La résolution taxonomique des données devrait être améliorée. Pour se faire, un échantillonnage est nécessaire afin de lier des spécimens physiques à des images. L'échantillonnage cependant doit rester ciblé et limité, en particulier sur des habitats vulnérables tels que les habitats coralliens. A termes, une base de données associant image, caractères morphologiques et ADN devrait être développée.

Outre la taxonomie, les spécimens échantillonnés pourraient servir à l'étude des réseaux trophiques afin de mieux comprendre le rôle fonctionnel des espèces de coraux.

La modélisation prédictive d'habitats

Les modèles prédictifs d'habitats produisent des cartes de distribution continue qui peuvent être particulièrement utiles en environnement profond où les données d'observation sont limitées (Howell *et al.*, 2011 ; Ross et Howell, 2013). Les modèles aident à prédire l'étendue d'une espèce ou d'un habitat sur laquelle pourrait s'appuyer les stratégies de préservation de la biodiversité (Howell *et al.*, 2011). Une limite de la modélisation prédictive d'habitat est la résolution à laquelle les données environnementales sont disponibles. Dans cette étude, le linéaire médian des habitats était compris entre 25 et 65 mètres. L'étendue spatiale des habitats est donc plus petite que la résolution de la bathymétrie et ses dérivés disponibles à une maille de 100 m pour le Golfe de Gascogne ainsi que la résolution des indicateurs hydrologiques disponible à une maille de 0.083° latitude (~10 km).

Les modèles prédictifs d'habitat seront développés dans le cadre du projet européen H2020 ATLAS (A Trans-Atlantic assessment and deep-water ecosystem-based spatial management plan for Europe). Ces modèles se concentreront sur des prédictions des niches potentielles des espèces dominantes de coraux, par exemple les scléractiniaires *L. pertusa*/ *M. oculata*, la pennatule *Kophobelemnion* cf. *stelliferum*, la gorgone *Narella versluysi*, et l'antipathaire *Leiopathes* sp. Ils pourront être utilisés pour guider de futures campagnes et aider au développement de plans de gestion environnementale. La niche potentielle et la niche réalisée des espèces coralliennes seront comparées en particulier avec l'empreinte des activités de la pêche sur les 10 dernières années pour évaluer des zones prioritaires qui auraient besoin de préservation ou réhabilitation.

Les implications pour la conservation

Les coraux d'eau froide sont des cibles importantes de conservation. Il est reconnu que les récifs de coraux en particulier ont besoin d'être préservés, mais d'autres habitats, par exemple les jardins de coraux, sont également listés comme des cibles de conservation. Les résultats de cette étude sont à la base de la délimitation de grands secteurs, prémices d'un réseau de sites Natura 2000 pour la préservation de l'habitat 'récif' au large sous la Directive Habitats Faune Flore

(MHNH-SPN et GIS-Posidonie, 2014). L'habitat 'récif', au sens de la Directive Habitats inclut les récifs, les jardins de coraux ainsi que les substrats durs colonisés en général. Le réseau Natura 2000 proposé sera la première mesure de protection qui se focalise sur les habitats benthiques dans les eaux profondes du Golfe de Gascogne. Cette étude a également souligné l'importance potentielle des habitats coralliens sur substrat meuble compte tenue de la diversité des communautés associées à ce type d'habitat. Ces habitats coralliens ne relèvent pas de la définition de l'habitat récif selon la Directive Habitat et ne feront donc pas l'objet de mesure de gestion à court terme. Indirectement, ces habitats bénéficieront néanmoins de la désignation des sites Natura 2000 puisqu'ils sont également présents dans les grands secteurs. Néanmoins, ces habitats de substrat meuble prédominent dans le sud du Golfe de Gascogne, sur la marge Aquitaine où aucun site Natura 2000 ne sera désigné (Fig. 1). D'autres stratégies que Natura 2000 devront donc être recherchées pour favoriser la préservation de ces habitats vulnérables dans la ZEE française en incluant le sud du Golfe de Gascogne. Le Directive Cadre Stratégie pour le Milieu Marin (DCSMM : 2008/56/EC) pourrait être une solution puisqu'un des objectifs est le maintien et la protection de la biodiversité des écosystèmes marins.

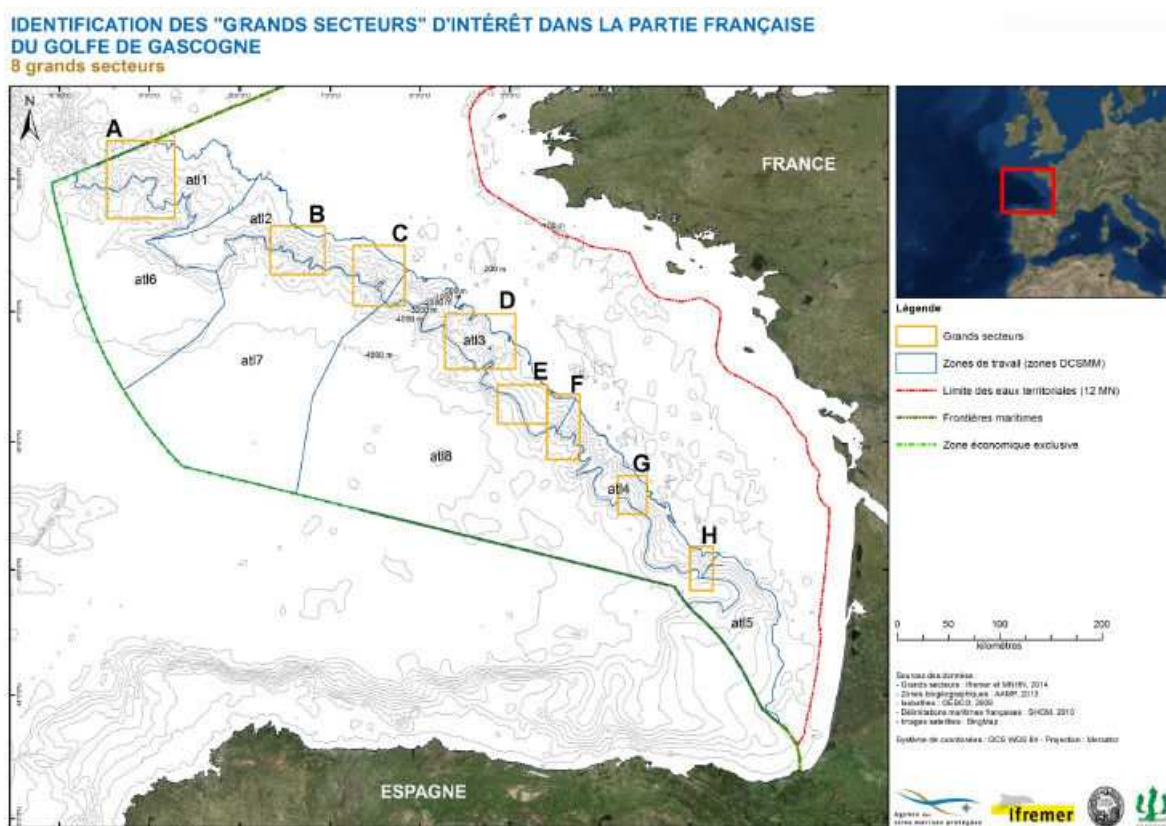


Figure 1 : Les grands secteurs du Golfe de Gascogne identifiés pour les habitats 1170 'récif' sous le Directive Habitats et proposés pour un réseau de Natura 2000. Secteurs A-H en jaune : les secteurs proposés, en bleu : les zones de travail définies par la DCSMM ; en vert : limites de la ZEE française ; en rouge : la limite des eaux territoriales (12 MN). Reproduit de MHNH-SPN et GIS-Posidonie (2014).

Résultats principaux

1. Les habitats coralliens sont **abondants et diversifiés**.
 - La distribution des habitats coralliens est hétérogène liée à l'interaction entre processus hydrodynamiques et processus sédimentaires, liée à la morphologie du canyon (par ex. la pente).
2. **Trois types d'habitat principaux** sont présents et se distinguent par la densité, la diversité et la composition taxonomique des communautés de coraux et leurs faunes associées.
 - Les habitats biogéniques sont des *hotspots* de diversité.
 - Les habitats sur substrat dur ont une diversité de coraux élevée.
 - Les habitats sur substrat meubles ont une diversité de faune associée élevée.
3. Les habitats coralliens sont **menacés par des activités humaines**.
 - Les déchets marins, particulièrement les plastiques, sont observés.
 - La pêche au chalut de fond pourrait contribuer à la prédominance des débris de coraux sur les interfluvés et le haut de pente contigu au plateau.
4. Les connaissances acquises sur la nature et la distribution des habitats coralliens ont servi de base à la création d'**un réseau Natura 2000** pour l'habitat 'récifs' dans les canyons du Golfe de Gascogne.

En plus, des articles publiés (chapitre 3 et 4, appendices I, II et III) et en préparation (chapitre 4), les données de cette étude ont contribué aux rapports et aux articles scientifiques suivants :

- Bajjouk, T., Menot, L., Van Den Beld, I., Tourolle, J., Fabri, M.-C., and Chauvet, P. (2015). Contributions au Référentiel National des Habitats Benthiques de la Région Atlantique. Identification et classification des habitats profonds. Fiches descriptives d'habitats. Rapport d'activités 2014. RST/IFREMER/DYNECO/AG/15-03/TB. 41 pp.
- Chan, T.-Y., Van Den Beld, I.M.J., and De Grave, S. (2016). A further record of the rare hippolytid shrimp *Leontocaris lar* Kemp, 1906 (Decapoda, Caridea) from the Celtic Sea, off north-western France. *Crustaceana* **89**(2), 251-257. doi: 10.1163/15685403-00003515.
- Fabri, M.-C., Pedel, L., Menot, L., and Van den Beld, I. (2013). Guide MIOP - Méthode pour l'acquisition d'Imagerie OPTique (MIOP) pour le suivi de l'Etat Ecologique des écosystèmes marins profonds benthiques. Doc. 2013-RST.ODE / LER-PAC / 13-29. Ifremer, La Seyne sur Mer, 22 pp.
- Gomes-Pereira, J.N., Auger, V., Beisiegel, K., Benjamin, R., Bergmann, M., Bowden, D., Buhl-Mortensen, P., De Leo, F.C., Dionísio, G., Durden, J.M., Edwards, L., Friedman, A., Greinert, J., Jacobsen-Stout, N., Lerner, S., Leslie, M., Nattkemper, T.W., Sameoto, J.A., Schoening, T., Schouten, R., Seager, J., Singh, H., Soubigou, O., Tojeira, I., van den Beld, I., Dias, F., Tempera, F., and Santos, R.S. (2016). Current and future trends

- in marine image annotation software. *Progress in Oceanography* **149**, 106-120. doi: 10.1016/j.pocean.2016.07.005.
- Menot, L., and Van den Beld, I. (2013). Nature, distribution et diversité des habitats de substrats durs du Golfe de Gascogne. Doc. 12/2013 - REM/EEP/LEP 13-35. Ifremer, Brest, 28 pp.
- Michez, N., Bajjouk, T., Aish, A., Andersen, A.C., Ar Gall, E., Baffreau, A., Blanchet, H., Chauvet, P., Dauvin, J.-C., De Casamajor, M.-N., Derrien-Courtél, S., Dubois, S., Fabri, M.-C., Houbin, C., Le Gall, L., Menot, L., Rolet, C., Sauriau, P.-G., Thiebaut, E., Tourolle, J., and Van den Beld, I. (2015). Typologie des habitats marins benthiques français de Manche, de Mer du Nord et d'Atlantique: version 2. Rapport SPN 2013 - 9. MNHN, Paris, 32 pp.
- MNHN-SPN, and GIS-Posidonie (2014). Méthodologie et recommandations pour l'extension du réseau Natura 2000 au-delà de la mer territoriale pour l'habitat récifs (1170): région biogéographique marine Atlantique. Rapport SPN 2014, 236 pp.
- Pedel, L., Fabri, M.-C., Menot, L., and Van den Beld, I. (2013). Mesure de l'état écologique des habitats benthiques du domaine bathyal à partir de l'imagerie optique. (Sélection de métriques et proposition d'une stratégie de surveillance). Doc. 2013-RST.ODE / LER-PAC / 13-10. Ifremer, La Seyne sur Mer, 44 pp.
- Ragnarsson, S.Á., Burgos, J.M., Kutti, T., van den Beld, I., Egilsdóttir, H., Arnaud-Haond, S., and Grehan, A. (2017). The impact of anthropogenic activity on cold-water corals. In: *Marine Animal Forests: The Ecology of Benthic Biodiversity Hotspots*, S. Rossi, L. Bramanti, A. Gori & C. Orejas (eds.). Springer International Publishing, Cham, 1-35. doi: 10.1007/978-3-319-17001-5_27-1.

Conclusions (English version)

This study reports new results on the distribution and diversity of coral habitats in the submarine canyons of the Bay of Biscay. The main objectives were: (i) to describe the heterogeneity and diversity of coral habitats on different spatial scales, (ii) to identify the factors controlling this distribution and the structuring species at a regional and local scale, (iii) to identify the diversity of the megafaunal community associated with these coral habitats as well as the abiotic and biotic factors influencing the community, and (iv) to describe potential impacts of human activities on coral habitats in the form of litter.

To meet these objectives, 24 canyons and 3 locations between 2 adjacent canyons were visited during 46 dives with an ROV or a towed camera. The image footage acquired by these optical techniques was analysed for habitat type, coral and non-coral organisms and coverage of biogenic, hard and soft substrate. Litter items were identified on image footage of 15 out of 24 canyons. The influences of biotic and abiotic factors on the distribution and structure of coral habitats, coral species and their associated fauna were investigated.

This study increases the knowledge about the distribution and diversity of coral habitats in the Bay of Biscay over a large spatial extent. Eleven coral habitats according to the CoralFISH classification system (Davies *et al.*, 2017) were observed and were constructed by 62 coral morphotypes belonging to the scleractinian, antipatharian, gorgonian and/or pennatulacean corals. This shows a high diversity of corals within the habitats. The faunal community associated with coral habitats is rich: a total of 191 morphotypes, of which 160 unique morphotypes, are observed to associate with one or more coral habitats.

Substrate drives the structure and composition of coral assemblages and associated fauna

Substrate type is an important factor driving patterns in both coral and associated megafaunal assemblages. A dichotomous distinction in coral assemblages – hard/biogenic substrate *versus* soft substrate – was observed. This dichotomy is caused by the need of either hard or soft substratum for the settlement of corals.

Hard substrate and biogenic habitats share similar compositions in coral species. The dominant reef-building scleractinians, however, differ. *Lophelia pertusa* and *Madrepora oculata* are dominant on the biogenic habitats and *Solenosmilia variabilis* on the colonial scleractinians on hard substrate habitat. On the contrary, a high coral species turnover between soft substrate habitats was observed. These habitats were mainly formed by the aggregation of one coral species belonging to the gorgonians, sea pens or solitary scleractinians. The cause of this high species turnover is unknown, but it may be explained by a number of factors. Firstly, the grain size or composition of the sediment might be important to corals that colonise soft substrate. It may be possible that sea pens, isidid gorgonians and solitary corals colonise only certain sediment types with particular grain sizes or compositions, due to the system of ‘attachment’ of these corals: a peduncle for sea pens, a hold-fast for isidid gorgonians or free from attachment

for solitary corals. Secondly, the presence of burrows made by megafauna, e.g. the langoustine *Nephrops norvegicus*, causing changes in sediment structure, can have an influence on coral settlement. Some seapens, e.g. *Funiculina quadrangularis*, are observed on areas with burrows and OSPAR has listed 'seapens and burrowing megafauna' as a threatened and/or declining habitat. However, the interaction between sea pens and *N. norvegicus* is unknown. Even though burrows were observed in this present study, they were not quantified and used as an explanatory variable in analyses. Thirdly, potential differences in dietary requirements between the coral orders may also explain the high species turnover between the soft sediment habitats, even though the diet of coral species remains largely unknown.

The importance of substrate type was also observed for the associated fauna. Three groups of associated faunal assemblages were observed: (i) assemblages associated with biogenic habitats dominated by the crinoid *Koehlermetra porrecta*, (ii) assemblages associated with hard substrate, dominated by brachiopods, and (iii) assemblages associated with soft substrate with a higher equitability between morphotypes and no dominant one. Therefore, the hypothesis that the composition of the associated fauna is driven by substrate type can be accepted. As coral species, associated fauna also has a preference in substrate type for settlement, contributing to this three-way distinction.

In addition, species competition for space and food is important for this pattern because it can cause the dominance of one species. This species competition is stronger in hard substrate habitats than in soft substrate habitats. Soft sediment habitat has a three-dimensional structure created by the possibility for individuals to bury themselves in the sediment. This reduces the competition for space and food between individuals and, thus, limits the pre-emption of a resource by one or a few dominant species on soft substrate habitats. A stronger species competition may also exist on biogenic habitat, although the biogenic habitats do have a three-dimensional structure. *K. porrecta* outcompetes other organisms for food and space. This filter-feeding crinoid benefits from the elevated position higher in the water column and thus in the current transporting food.

Hydrodynamics and sedimentary regimes drive the distribution of coral habitats at regional and local scales

The observed distribution of coral habitats is heterogeneous at the scale of the Bay of Biscay: a dominance of soft substrate coral habitats on the Aquitaine margin is observed and live scleractinian habitats are absent on this margin and on the southern Armorican margin. At the canyon scale, the distribution of habitats is also heterogeneous: scleractinian occurrences were higher on the north-western flank and sea pens occurred more frequently on the south-eastern flank.

The distribution at both scales could be explained by the dominant substrate type, resulting from the interplay of hydrodynamic and sedimentation processes: strong currents erode the seafloor exposing hard substrate whereas high sedimentation rates result into soft sedimentary bottoms, especially in combination with low current speeds. The observed heterogeneous distribution on the basin scale is probably the result of this interplay: the canyons incising the

Aquitaine margin exhibit a smoother topography, higher sedimentation rates and weaker currents favouring the existence of soft substrate coral habitats. The observations on a canyon scale could also be related to the hydrodynamics and the dominant substrate type; a dominant current in the Bay of Biscay erodes the north-western flank favouring scleractinians compared to the more sedimentary south-eastern flank favouring soft substrate habitats.

The influence of geographical, geomorphological and oceanographic factors: A matter of resolution?

Prior to analysis, depth, latitude, temperature, salinity, substrate type and measures of slope and rugosity were hypothesised to influence the distribution of coral habitats and structuring species. This hypothesis can neither be accepted nor rejected.

Besides the described influence of substrate type, slope also has an influence on the distribution of coral habitats as could be observed using the geomorphological classes. Live coral habitats tend to occur on areas with slopes steeper than 10° and more in the canyon, whereas coral rubble is more frequent on flatter areas with slopes less than 10° and on the interfluves and upper slope of the canyons. The influence of slope is stronger for biogenic and hard substrate habitats than for soft substrate habitats.

Depth, latitude, temperature, salinity or measures of rugosity did not discriminate the specific coral habitats in this study: the coral habitats have similar environmental settings at the resolution at which these environmental factors are available in this study. The resolution of the environmental factors is much coarser than the resolution of the habitats in this study and may limit outcomes of species distribution or habitat suitability models.

Coral reefs and coral habitats on soft sediment are hotspots of biodiversity

The comparison of the faunal communities of different coral habitats with each other revealed the following patterns: (i) densities of fauna associated with reef are higher than the densities of fauna associated with the other scleractinian habitats, (ii) the mean species richness per image of coral reef is higher than coral rubble habitat, (iii) the regional diversity observed for biogenic habitats is higher than that of hard substrate habitats, (iv) the local and regional diversities of soft substrate habitats is similar or even higher than the diversities observed on hard substrate and biogenic habitats, and (v) a negative relationship between coral diversity and the diversity of the associated species.

The high density on coral reefs and the high regional diversity on biogenic habitats support the hypothesis that coral reefs are biodiversity hotspots in submarine canyons of the Bay of Biscay and that they would support an associated faunal community that is dense and diverse. On a regional scale, the diversity of biogenic habitats is also higher than that of hard substrate habitats, also supporting that coral reefs and in this case also the other biogenic habitats, are biodiversity hotspots. The three-dimensional framework of reef-forming scleractinians creating a complex structure and increasing the heterogeneity of the habitat may explain the high diversity in biogenic habitats.

Surprisingly, both the local and regional diversity of the associated fauna on soft substrate habitats was high, while it was hypothesized that these habitats have the least diverse associated community. Moreover, the actual densities and diversity on this type of habitat are likely underestimated, since only the epifauna has been observed. These findings, thus, do not support the hypothesis of lower densities and diversities of the fauna associated with soft substrate habitats compared to biogenic and hard substrate coral habitats. Although the sample sizes of the soft substrate habitats are not large enough to conclude, the results of this study are promising and suggest that these habitats need more attention from scientific and management perspectives.

Cold-water corals are threatened by human activities

This study gives a description of the litter distribution in 15 canyons of the Bay of Biscay. Plastic items were the most abundant items observed on image footage, followed by material related to the fishing industry, e.g. nets and longlines. A spatially heterogeneous distribution was observed that could be related to the sources of the items, potential hydrodynamics existing in canyons and the shape and sedimentation of the canyons. The seafloor relief formed by biological and geological features, e.g. corals and boulders, is able to stop litter from moving, especially soft plastics, and has, therefore, also an influence on the litter distribution.

Litter can impact corals in different ways, such as suffocation and entanglement. The results of this study show that litter and corals can co-occur: (i) litter items, especially plastics, are accumulated in areas with a high seafloor relief, caused by corals and geological features, and (ii) litter was most abundant in a depth range where most coral habitats are also observed. This may have implications to conservation, although it is a challenge to quantify the impact of litter on corals.

Differences in distributions of coral reefs and coral rubble may be in part related to the fisheries industry. The occurrence of coral reefs was skewed towards deeper and steeper areas than coral rubble. Shallower and flatter areas, especially the upper slope and parts of the interflaves, are easier to access with bottom trawls than steeper and deeper areas in the canyons. These observations support the hypothesis that canyons may function as natural refuges (Fernandez-Arcaya *et al.*, 2017; Huvenne *et al.*, 2011).

Perspectives (English version)

This study brings us a step closer to the understanding of the distribution of cold-water habitats in the Bay of Biscay and to evaluate the associated biodiversity and community structure. However, some questions remain or new questions have arisen. It is necessary to fully understand the environmental control of cold-water corals and their habitats to be able to understand why in certain places coral colonies can develop to a habitat and in other places these colonies do not form a habitat. Furthermore, this understanding will also bring us answers why coral reefs can develop to very high, large pristine reefs with a high proportion of live colonies while in other areas coral reefs are low with a higher proportion of dead framework, e.g. off the Norwegian shelf break or carbonate mounds off Ireland *versus* the canyons of the Bay of Biscay.

Sampling effort and design

In this study, as in most of the studies dedicated to CWCs, the sampling effort among the observed habitats was not equal. Several cruises and dives targeted coral reef and rubble, thus biasing the sampling. The sample sizes of the hard substrate habitats, especially those created by antipatharians or gorgonians, as well as the soft substrate habitats are much smaller. Collecting additional data of these undersampled habitats would contribute to the understanding of the distribution and diversity of both coral and associated fauna assemblages. This could also result in a confirmation of the unexpected high diversity of the faunal community associated with soft substrate habitats.

Additional dives could be performed on the southern Armorican and Aquitaine margins where sampling was rather low compared to the Celtic margin and northern and central Armorican margin. Furthermore, additional dives could be performed in depth strata deeper than 1500 m, since images are rarely collected deeper than this water depth, while the canyons are much deeper.

Although the geomorphological classes were used to compare occurrences of habitats between flanks, slope classes and location (canyon, interfluves and upper slope), not all geomorphological classes, e.g. canyon banks and interfluves terraces, could be tested separately, due to low sample sizes of rare classes. Due to the expert interpretation used for the establishment of the geomorphological classes, it gives more information than only the bathymetry or the slope. The link between geomorphology and corals can aid understanding the distribution, but it can also be used in future research and cruise planning targeting specific coral habitats increasing the chance to actually observe these habitats on the seafloor. For similar reasons, it could guide the conservation of cold-water corals in areas where observations are absent.

An additional sampling design would be a focus study on one canyon to investigate the distribution and ecology of coral habitats on a smaller scale. A similar sampling design was carried out within Whittard Canyon, a canyon incising the Celtic margin, just north of the study area of this study. Multiple dives were performed in each of the four main branches of this canyon and include both observations of corals by ROVs and measures on hydrodynamics and

sedimentation by using different instruments, e.g. CTDs, and sediment traps. It is challenging to measure and understand the hydrodynamics and sedimentation in canyons, because these are complex processes that are also influenced by the local topography. Such sampling could also be done in canyons of this study. The Odet Canyon, for which the sampling effort is already large and seven coral habitats are observed, would be a good candidate for an extensive and high-resolution mapping and sampling program.

The taxonomic resolution of the data should be improved. To reach this goal, sampling is necessary in order to link the physical specimen to images. The sampling, however, should be limited and targeted to certain specimens, especially in vulnerable habitats such as cold-water coral habitats. Eventually, a database associating images, morphological characteristics and DNA sequences needs to be developed.

In addition to taxonomy, the collected specimens could be used to study food webs in order to better understand the functional role of coral species.

Habitat suitability modelling

Habitat suitability modelling provides a method to create species distribution maps without gaps and is particularly useful in the deep sea where observation data is limited (Howell *et al.*, 2011; Ross and Howell, 2013). The continuous models help to understand the extent of a species or habitat and may identify areas of conservation interest (Howell *et al.*, 2011). One of the limitations of habitat suitability modelling is the resolution at which the environmental predictors are available. In this study, the median linear of the habitats ranged between 25 to 65 meters. These sizes are smaller than the resolution of the bathymetry and the derivatives available for the whole Bay of Biscay that was 100 m. The resolutions of the hydrological predictors are not even close to the habitat sizes.

A habitat suitability model will be created as part of the European Commission Horizon2020 funded project ATLAS (a transatlantic assessment and deep-water ecosystem-based spatial management for Europe; grant-agreement no. 678760). This model will focus on the predictions of the potential niche of several coral species among the dominant ones in each habitat, e.g. the scleractinians *L. pertusa*/ *M. oculata*, the pennatulacean *Kophobelemnon* cf. *stelliferum*, the gorgonian *Narella versluysi* and the antipatharian *Leiopathes* sp. Habitat suitability models predict the potential niche of cold-water coral habitats and can be used to guide future cruises, but also conservation plans and marine management. The potential and realised niches of the coral species will in particular be compared with the footprint of fishing activities over the past 10 years in order to assess priority areas in need of preservation or remediation.

Implications for conservation

Cold-water corals are important conservation targets. It is recognised that especially coral reefs need to be protected, but other habitats, e.g. coral gardens, are also listed as targets for conservation. The results of this study already formed the scientific basis for a proposal to define sectors for a network of Natura 2000 sites to protect ‘reef’ habitat under the Habitats Directive, including coral reefs, coral gardens and other hard substrate habitats including those

that are formed by non-corals. Moreover, this study underlines the potential importance of coral habitats dominated by soft substrate for associated fauna considering the high diversity of the community associated with this type of habitats. This shows that coral habitats on soft substrate that do not fit the definition of reefs in the Habitats Directive could also be important candidates for protection. Indirectly these habitats will nevertheless benefit from the designation of the Natura 2000 sites, since they also present in the major sectors. Nevertheless, soft substrate dominated coral habitats dominate in the southern Bay of Biscay, on the Aquitaine margin, where no Natura 2000 sites will be designated (Fig. 1). Other strategies than Natura 2000 should be sought to preserve these vulnerable habitats in the French EEZ and would include the South Bay of Biscay. The MSFD (MSFD: 2008/56/EC) could be a solution as one of the objectives is maintaining and protecting the biodiversity of marine ecosystems.

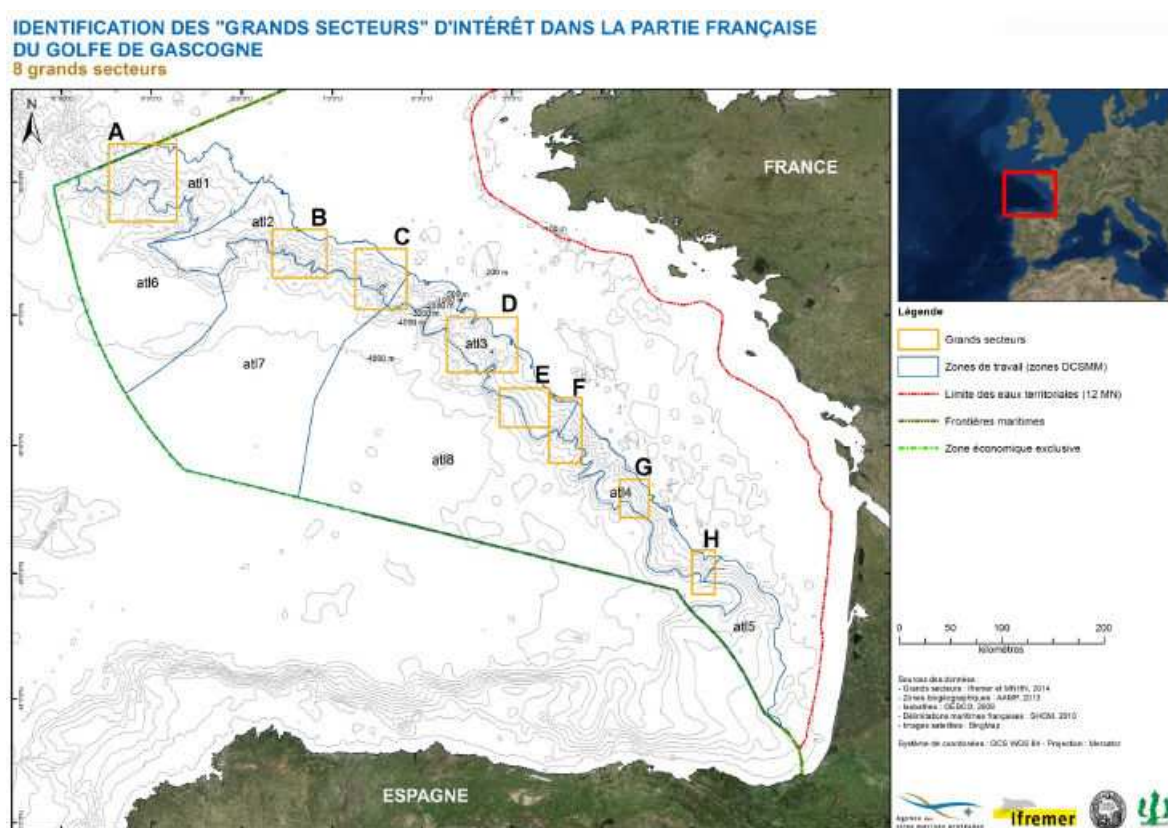


Figure 1: The sectors identified for the Bay of Biscay for the 1170 reef habitats under the EC Habitats Directive and proposed for a Natura 2000 network. Yellow sectors A – H: proposed sectors; blue: work zones defined by the MSFD; green: the French EEZ; red: limit of the territorial waters (12 nm). Reproduced from MHNH-SPN and GIS-Posidonie (2014).

Key-findings

1. Coral habitats are **abundant and diverse**.
 - Coral habitats have a heterogeneous distribution linked with the interplay of hydrodynamic and sedimentation processes; this interaction is mediated by the canyon morphology (e.g. slope).
2. **Three main types of coral habitats** were present and are distinguished by the density, the diversity and the taxonomic compositions of the coral communities and their associated fauna.
 - Biogenic habitats are biodiversity hotspots.
 - Hard substrate habitats have a high coral diversity.
 - Soft substrate habitats have a high associated fauna diversity.
3. Coral habitats are **threatened by human activities**.
 - Marine litter, especially plastics, was observed.
 - Trawling could contribute to the dominance of coral rubble on the interflaves and the upper slope.
4. The acquired knowledge on the nature and the distribution of coral habitats served as the scientific basis used to create a **Natura 2000 network** of ‘reef’ habitats in the Bay of Biscay

Besides the papers that have been published (chapters 3 and 5, appendices I, II and III) or are in preparation (chapter 4), data of this thesis contributed to the following reports or scientific papers:

- Bajjouk, T., Menot, L., Van Den Beld, I., Tourolle, J., Fabri, M.-C., and Chauvet, P. (2015). Contributions au Référentiel National des Habitats Benthiques de la Région Atlantique. Identification et classification des habitats profonds. Fiches descriptives d’habitats. Rapport d’activités 2014. RST/IFREMER/DYNECO/AG/15-03/TB. 41 pp.
- Chan, T.-Y., Van Den Beld, I.M.J., and De Grave, S. (2016). A further record of the rare hippolytid shrimp *Leontocaris lar* Kemp, 1906 (Decapoda, Caridea) from the Celtic Sea, off north-western France. *Crustaceana* **89**(2), 251-257. doi: 10.1163/15685403-00003515.
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- Pedel, L., Fabri, M.-C., Menot, L., and Van den Beld, I. (2013). Mesure de l'état écologique des habitats benthiques du domaine bathyal à partir de l'imagerie optique. (Sélection de métriques et proposition d'une stratégie de surveillance). Doc. 2013-RST.ODE / LER-PAC / 13-10. Ifremer, La Seyne sur Mer, 44 pp.
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Annex I

Fernandez-Arcaya, U., Ramirez-Llodra, E, Aguzzi, J., Allcock, A.L., Davies, J.S., Dissanayake, A., Harris, P., Howell, K., Huvenne, V.A.I., Macmillan-Lawler, M., Martín, J., Menot, L., Nizinski, M., Puig, P., Rowden, A.A., Sanchez, F and **Van den Beld, I.M.J.** (2017). Ecological role of submarine canyons and need for canyon conservation: a review. *Frontiers in Marine Science* **4**(5). Doi: 10.3389/fmars.2017.00005



Ecological Role of Submarine Canyons and Need for Canyon Conservation: A Review

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Submarine canyons are major geomorphic features of continental margins around the world. Several recent multidisciplinary projects focused on the study of canyons have considerably increased our understanding of their ecological role, the goods, and services they provide to human populations, and the impacts that human activities have on their overall ecological condition. Pressures from human activities include fishing, dumping of land-based mine tailings, and oil and gas extraction. Moreover, hydrodynamic processes of canyons enhance the down-canyon transport of litter. The effects of climate change may modify the intensity of currents. This potential hydrographic change is predicted to impact the structure and functioning of canyon communities as well as affect nutrient supply to the deep-ocean ecosystem. This review not only identifies the ecological status of canyons, and current and future issues for canyon conservation, but also highlights the need for a better understanding of anthropogenic impacts on canyon ecosystems and proposes other research required to inform management measures to protect canyon ecosystems.

Keywords: submarine canyons, ecosystem service, anthropogenic impacts, conservation, management

INTRODUCTION

As resources on land are increasingly depleted, humanity is turning to the oceans, as never before, for new sources of food and materials (Ramirez-Llodra et al., 2011). A complex and mixed interplay of impacts resulting from fisheries, oil and gas operations, mining practices, and many other anthropogenic activities, have caused unintended damage to ecosystems (Davies et al., 2007). This, in turn, may affect the supply of targeted resources, as well as impact other ecosystem services. This scenario hinders the achievement of UN Millennium Assessment goals relating to human wellbeing, including having sufficient food at all times and having a healthy physical

environment (MA, 2005). Therefore, the identification and protection of key marine habitats, especially those that substantially contribute to important ecological services (e.g., nutrient cycling, carbon sequestration, fisheries, nursery grounds, and habitat support) must become a priority.

The deep sea, the largest biome on Earth, is composed of a variety of different habitats with specific biotic and abiotic characteristics (Ramirez-Llodra et al., 2010). Submarine canyons are one of these habitats. Recent novel technological developments including underwater acoustic mapping, imaging, and sampling technologies, and long-term/permanent moored or benthic observatories, have greatly contributed to our understanding of the diverse and complex hydrodynamics (Xu, 2011) and geomorphology of canyons over the last two decades (Robert et al., 2014; Quattrini et al., 2015), allowing the spatio-temporal tracking of oceanographic processes and the associated biological responses, with an integration level that grows every day (Aguzzi et al., 2012; Matabos et al., 2014). As a result of prospective surveys, we know that submarine canyons are major geomorphic features of continental margins, with more than 9000 large canyons covering 11.2% of continental slopes globally (Harris et al., 2014), with an estimated accumulated axis length of over 25,000 km (Huang et al., 2014). Canyons are characterized by steep and complex topography (Shepard and Dill, 1966; Lastras et al., 2007; Harris and Whiteway, 2011) that influences current patterns (Shepard et al., 1979; Xu, 2011) and provides a heterogeneous set of habitats, from rocky walls and outcrops to soft sediment (De Leo et al., 2014). These geomorphologic features act as preferential particle-transport routes from the productive coastal zone down continental slopes to the more stable deep seafloor (Allen and Durrieu de Madron, 2009; Puig et al., 2014).

Canyons have been described as “keystone structures” (Vetter et al., 2010) because of their role as relevant sources of goods and services to human populations. An increasing amount of data provides evidence of how canyons act benefiting and supporting fisheries (Yoklavich et al., 2000; Company et al., 2012), and enhance carbon sequestration and storage (Epping et al., 2002; Canals et al., 2006; Masson et al., 2010). Canyon habitats also provide nursery (Sardà and Cartes, 1994; Hoff, 2010; Fernandez-Arcaya et al., 2013) and refuge sites for other marine life (Tyler et al., 2009; De Leo et al., 2010; Vetter et al., 2010; Morris et al., 2013), including vulnerable marine ecosystems and essential fish-habitats such as cold-water corals and sponge fields (Schlacher et al., 2007; Huvenne et al., 2011; Davies et al., 2014). Canyons have also been shown to provide habitat for spawning females of pelagic and benthic species of commercial interest (Farrugio, 2012). Other faunal components of marine ecosystems, including mammals and marine birds, also use canyons, for example, as feeding grounds (Abelló et al., 2003; Garcia and Thomsen, 2008; Roditi-Elasar et al., 2013; Moors-Murphy, 2014). Habitat diversity and specific abiotic characteristics enhance the occurrence of high levels of biodiversity in some canyons (Vetter and Dayton, 1998; McClain and Barry, 2010; Company et al., 2012; De Leo et al., 2014). Because of this biodiversity, canyons can be a rich source of genetic resources and chemical compounds (i.e., the use

of canyon organisms in biotechnological, pharmaceutical, or industrial applications, Jobstvogt et al., 2014).

The steep slopes and rocky topography have limited exploitation of seafloor resources within canyons through activities such as bottom-trawl fishing (Würtz, 2012). Consequently, many canyon areas experience lower levels of anthropogenic pressure than adjacent areas on the shelf and slope. Nevertheless, submarine canyons are increasingly subjected to different stressors, not only in relation to fishing (Company et al., 2008; Martín et al., 2008; Orejas et al., 2009; Puig et al., 2012), but also to oil and gas extraction (Harris et al., 2007). Moreover, the hydrodynamic processes of canyons enhance the transport of litter (Mordecai et al., 2011; Ramirez-Llodra et al., 2013; Tubau et al., 2015) and chemical pollutants from the shelf to deep-sea environments (Palanques et al., 2008; Koenig et al., 2013; Pham et al., 2014). Canyons have also been used as dumping areas for tailings of land-based mining (Hughes et al., 2015; Ramirez-Llodra et al., 2015). Additionally, effects of climate change may affect the physical and chemical characteristics of water masses, modifying the intensity of currents (Canals et al., 2009). These modifications may seriously impact the structure and functioning of canyon communities and have important implications for nutrient supply to the deep-ocean ecosystem (Solomon, 2007; Levin and Le Bris, 2015) as well as for carbon storage (Epping et al., 2002; Masson et al., 2010). Thus, anthropogenic threats to submarine canyons demand urgent responses to ensure sound ecosystem-based management of human resources based on robust scientific data that will guarantee both the development of local and regional economies and the long-term sustainability of ecosystems and the services they provide.

The aims of this review are to: (1) highlight current scientific knowledge concerning canyon ecosystems; (2) describe our current understanding of the role played by canyons in providing ecosystem goods and services; (3) identify the impacts to which canyons are increasingly being subjected; (4) review current frameworks and strategies for protecting canyons, and assess the extent of current canyon conservation worldwide; before finally, (5) identifying directions for future canyon research, with a focus on the conservation needs of canyons. This review is based on published literature and expert knowledge, and is the result of discussions held during the 2014 International Network for submarine Canyon Investigation and Scientific Exchange workshop (INCISE, www.incisenet.org, Huvenne and Davies, 2014).

THE ECOLOGICAL ROLE OF CANYONS

The interplay between canyon topography and oceanic currents has profound consequences for the diversity, functioning, and dynamics of both pelagic and benthic communities. For example, currents funneled through canyons likely enhance primary productivity (Ryan et al., 2005) and drive sediment transport and associated particle-reactive substances toward deep environments (Puig et al., 2014). Higher levels of primary productivity may lead to canyons being hotspots of faunal

productivity in the deep sea (De Leo et al., 2010). The highly variable seascapes within a canyon support diverse assemblages of species that play a wide variety of ecological roles, often across small spatial scales, giving rise to enhanced biodiversity, and ecosystem function (McClain and Barry, 2010). Given their local importance, canyons represent a relevant regional source of marine biodiversity and ecosystem function (Leduc et al., 2014).

Canyon Effects on Local Circulation and Sedimentation

On many continental margins, cross-shelf exchanges of water, and particulate matter are inhibited by the presence of density fronts and associated slope currents flowing parallel to the isobaths (e.g., Font et al., 1988). Submarine canyons intercept the path of these currents, inducing a new dynamic balance, eventually enhancing non-geostrophic motions, and shelf-slope exchanges (Huthnance, 1995). Near the seafloor, alignment of the current with the direction of the canyon axis is commonly observed (Shepard et al., 1979; Puig et al., 2000). The adjustments of the current to the canyon topography produce vortex stretching and vertical motions (Klinck, 1996; Hickey, 1997). These modifications of the currents may result in local upwelling, which pumps nutrients to the euphotic zone and thus stimulates primary production (Ryan et al., 2005). Additionally, closed-circulation cells and downwelling may develop over canyons, enhancing the capacity of the canyon to trap particles transported by long-shore currents (Granata et al., 1999; Palanques et al., 2005; Allen and Durrieu de Madron, 2009). When thermohaline stratification of the water column is strong, the flow in the upper mixed layer may decouple from the underlying water levels, which interact with the rims of the canyon. In such a scenario, the current flowing above the canyon head tends to follow its path, ignoring the bottom topography, while the flow below the rim is deflected by the canyon (e.g., Palanques et al., 2005). This current flow can also induce the formation and focussing of internal waves (e.g., Hall and Carter, 2011).

Most of the particulate organic matter introduced into the marine environment by riverine inputs and coastal surface productivity, particularly the most labile fraction, is mineralized after several cycles of seafloor deposition/resuspension on the continental shelf. In contrast to this scenario, canyons act as morphological shortcuts, accelerating the transit of particles from fertile coastal and inner shelf environments toward the deep sea, thus enhancing the role of canyons as sedimentary depocentres, where enhanced oxidation and burial of organic carbon occurs (Epping et al., 2002; Masson et al., 2010). Additionally, large storm waves, hyperpycnal flows, dense shelf-water cascades, earthquakes, and other processes trigger mass failures of unstable deposits within canyon heads and on the shelf-edge areas of shelf-incising canyons (reviewed in Puig et al., 2014). Sediments (and associated organic matter) entrained in turbidity flows are exported from the canyon system for deposition on adjacent submarine fans (Talling, 2014). Thus, particle fluxes and sediment accumulation rates have been found to be much larger inside submarine canyons than in the adjacent

non-dissected margin at comparable depths (Martín et al., 2006; Zúñiga et al., 2009).

Canyon Effects on Pelagic and Motile Benthic or Demersal Fauna

In the pelagic realm, the diversity, and complexity of food webs increase in response to canyon-induced upwelling of nutrients. The high level of primary production attracts pelagic-associated secondary and tertiary consumers. Abundances of megafaunal species, including a variety of demersal fishes, large pelagic predators such as tuna, swordfish, and sharks, as well as cetaceans and birds, are enhanced. All these predators are likely to be present in canyon areas for feeding and breeding, albeit intermittently in some cases (Rennie et al., 2009). For example, demersal fishes, such as macrourids and cusk (*Brosme brosme*), in Baltimore and Norfolk canyons (NW Atlantic), prey upon large swarms of euphausiids and amphipods as well as benthic species, such as brittle stars, which are abundant because of canyon-enhanced productivity (Ross et al., 2015). In addition, canyons may concentrate motile megafauna that leave the adjacent slope in an attempt to evade visual predators by hiding within the complex canyon topography (Farrugio, 2012). Doya et al. (2014) recorded high numbers of sablefish (*Anoplopoma fimbria*) along Barkley canyon walls at approximately 900 m depth from the NEPTUNE Ocean Observatory, Canada. Canyon geomorphology can trap diel vertical migrants, such as hyperiid amphipods and euphausiids, when wind-generated currents push animals toward the canyon heads (Macquart-Moulin and Patriti, 1996). These trapped individuals regain their original depth position by swimming along the seabed, adopting a more nekto-benthic mode of movement, in order to restart a new vertical migration cycle (Aguzzi and Company, 2010).

The accumulation of organic matter, caused by the physical and geological characteristics of some submarine canyons, promotes higher abundances, biomass, and diversity of organisms compared to the adjacent open slope (**Figure 1**). These conditions have been observed at eutrophic canyons along continental margins (Brodeur, 2001) as well as in those associated with oligotrophic conditions on oceanic islands (De Leo et al., 2012). Elevated sedimentation rates inside submarine canyons can favor benthic detritivores (Puig et al., 2015) and fauna capable of rapidly conveying the organic material produced in the upper water column (Bianchelli et al., 2010), thereby processing large amounts of carbon for input into the benthic food web (Vetter and Dayton, 1998; De Leo et al., 2010; van Oevelen et al., 2011). Canyons can also influence the depth distribution and population structure of particular species during the various stages of its life cycle, thus affecting the distribution of biomass and density of specific life stages. For example, in some fishes (e.g., monkfish *Lophius piscatorius*, hake *Merluccius merluccius*), larger spawning females have been more commonly observed inside submarine canyons (e.g., Petit-Rhône and Grand-Rhône) than on the adjacent open slope (Farrugio, 2012). Additionally, canyons can act as recruitment grounds for some species of fishes and crustaceans. High abundances of egg cases of an unknown species of scyliorhinid catshark were found among coral in

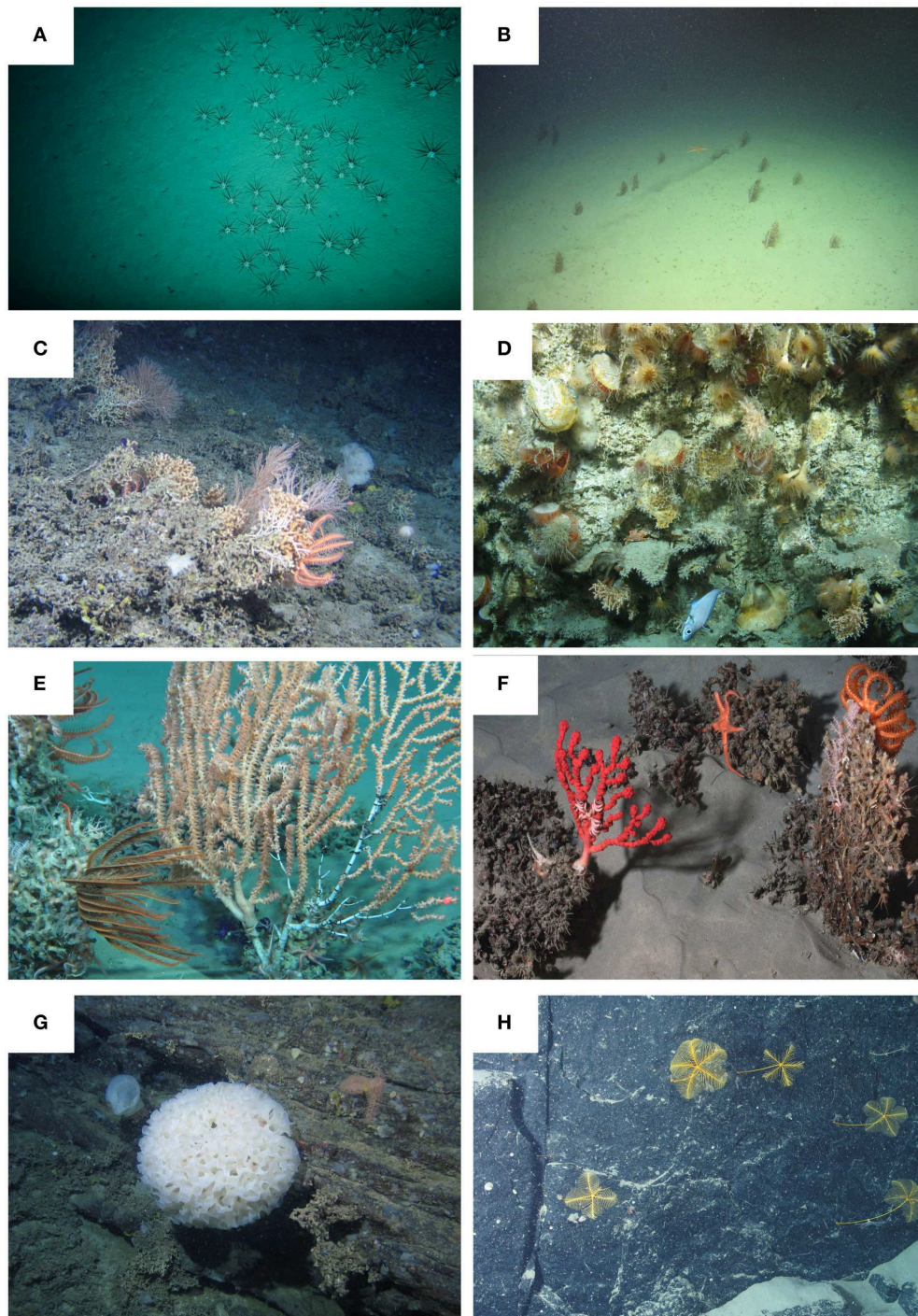


FIGURE 1 | Images showing diversity of habitats in submarine canyons. (A) An aggregation of the echinoid *Cidaris cidaris* on soft sediment in a Bay of Biscay canyon (NE Atlantic). Copyright: Ifremer, Evhoe 2011. **(B)** Field of the sea pen *Kophobelemnion* at approximately 750 m in Whittard canyon. Cruise CE14009. **(C)** Coral habitat at approximately 1500 m in an unnamed canyon north of the Porcupine Bank showing a brisingid seastar, *Solenosmilia* coral, bamboo coral, and white and yellow sponges. Cruise CE10004. **(D)** Biotope at 633 to 762 m depth on a vertical wall in Whittard Canyon dominated by large limid bivalves, *Acesta excavata* and oyster *Neopycnodonte zibrowii*. The scleractinian corals *Madrepora oculata* and *Desmophyllum* are also present. Cruise CE12006 **(E)** Cold-water coral community at about 1800 m in Whittard Canyon with bamboo coral in the foreground and *Solenosmilia* to the left. The crinoid is *Koehlermetra* and orange brisingids are top left. Cruise CE14009. **(F)** Cold-water coral community in a canyon in the Bay of Biscay. Dead framework of a colonial scleractinian is colonized by a *Paragorgia* and an unidentified gorgonian as well as many ophiuroids and a brisingid asteroid. Copyright: Ifremer, BobEco cruise 2011. **(G)** A hexactinellid sponge, probably the genus *Farrea* in an unnamed canyon north of Porcupine Bank. CE13008 cruise. **(H)** Stalked crinoid *Anachalypsicrinus neferti* on a vertical wall in a Bay of Biscay canyon. Copyright: Ifremer, BobEco cruise 2011. Images **(B–E,G)** taken by ROV Holland I, deployed from RV Celtic Explorer. Copyright NUI Galway / Marine Institute.

Mississippi Canyon, Gulf of Mexico (Etnoyer and Warrenchuk, 2007). In the Gulf of Lions (NW Mediterranean), periodic dense shelf-water cascading events supply large amounts of organic material to bathyal and abyssal areas (Canals et al., 2006; Pasqual et al., 2010). Recruitment of the highly mobile deep-sea shrimp *Aristeus antennatus* is enhanced in years following such events (Company et al., 2012). In Blanes Canyon (NW Mediterranean), benthic, and intermediate nepheloid layers, with significant amounts of suspended sediment, are present year round. There is evidence that the juveniles of some deep-sea shrimps (*Plesionika heterocarpus*, *P. edwardsi*, *P. giglioli*, and *P. martia*) and fishes (*Phycis blennoides*, *Mora moro*, *Lepidion lepidion* amongst others) concentrate in the benthic intermediate nepheloid layers this canyon, which act as a nursery area for these species (Puig et al., 2001; Fernandez-Arcaya et al., 2013).

Canyon Effects on Benthic Sessile Fauna and Infauna

In the benthic realm, enhanced primary production and current regimes provide suitable ecological niches for large and abundant suspension and filter feeders, such as sponges and cold-water corals (Figure 1). Resuspension of particulate organic matter (POM), combined with a slower deposition of particulate matter descending from the euphotic zone, leads to higher levels of particulates and nutrients in the water column inside canyons (Bosley et al., 2004), resulting in enhanced primary productivity. Suspension feeders and demersal planktivores likely benefit from these high concentrations of primary producers (Vetter et al., 2010). In Whittard Canyon (Celtic Margin of the NE Atlantic), accelerated currents increase the organic matter influx and therefore the availability of food compared to less active areas on the continental slope (Morris et al., 2013; Palmas et al., 2015). In the upper region of Whittard Canyon (~700 m depth), a very dense assemblage of corals and large bivalves was observed associated with a nepheloid layer that might provide a significant amount of food (Johnson et al., 2013). Furthermore, the scleractinian coral *Lophelia pertusa* was observed at great depth and higher densities in this canyon, than usually recorded in the NE Atlantic (Huvenne et al., 2011). The deepening of the distribution of *L. pertusa* could be related to downslope transport processes in canyons (Dullo et al., 2008). Likely mechanisms for food transport include hydrodynamic processes such as gravity currents and internal waves, or by the trapping effect of the canyon topography itself (Huvenne et al., 2011; Morris et al., 2013; Amaro et al., 2016). Similarly, high densities of gorgonians, pennatulids, and sponges in Pribilof and Zhemchug canyons (Bering Sea) may be supported by enhanced levels of primary productivity delivered by strong currents (Miller et al., 2012). Likewise, canyons intersecting the shelf break in East Antarctica, experience strong currents and particle fluxes and support dense communities of corals and sponges (Post et al., 2010).

Patches of detritus have been described as hotspots of food resources in canyons. These patches not only support locally high numbers of deposit feeders that benefit from the accumulation of macrophyte detritus, but also a variety of

crustaceans associated with down-welling (Vetter, 1995; Okey, 1997). Overall, the presence of detritus patches in canyons provides an additional food source, contributing to higher densities, and biomass of infauna in canyon sediments than in sediments on the adjacent shelf and slope (Vetter and Dayton, 1998). Bianchelli et al. (2010) examined meiofaunal assemblages in five submarine canyons and adjacent slope habitats along Portuguese, Catalan, and Adriatic margins. Their results suggest that available food sources, including detritus, as well as topographic and hydrodynamic features of canyons, influence meiofaunal abundance and biomass.

Within canyons, the complex topography alters current regimes and therefore, sediment-transport processes, influencing the patchy distribution of large sessile megafauna. The dissymmetric distribution and abundance of corals between opposite flanks of a canyon is a common feature reported from Lacaze-Duthiers, Cassidaigne, and Cap de Creus canyons in the Mediterranean Sea (Orejas et al., 2009; Fabri et al., 2014), Guilvinec, Penmarc'h, and Whittard canyons in the NE Atlantic (De Mol et al., 2011; Morris et al., 2013; Robert et al., 2014) and The Gully in the NW Atlantic (Mortensen and Buhl-Mortensen, 2005). Similarly, distribution of corals and sponges at the heads of shelf-incising canyons seems to be related to strong currents that expose underlying bedrock in these areas (De Mol et al., 2011). At a smaller scale, steep features of exposed rock, such as vertical walls and overhangs, facilitate the settlement of the scleractinian corals *L. pertusa* and *Madrepora oculata* (Freiwald et al., 2009; Huvenne et al., 2011; Gori et al., 2013; Morris et al., 2013; Davies et al., 2014; Fabri et al., 2014).

In addition to currents and topography, substrate heterogeneity is a key factor contributing to the highly diverse faunal assemblage present in submarine canyons (De Leo et al., 2014). Submarine canyons host a wide variety of substrate types, including mud, sand, hardground, gravel, cobbles, pebbles, boulders, and rocky walls, occurring either separately or in various combinations (Baker et al., 2011, Figure 2). Most species are restricted to either hard substratum (most scleractinians, antipatharians, most gorgonians, most sponges) or soft substratum (most pennatulids, some scleractinians, some gorgonians, some sponges). For example, in Pribilof and Zhemchug canyons (Bering Sea), gorgonians, and sponges were associated with hard substrate, while pennatulids were associated with soft sediment (Miller et al., 2012). In Bari Canyon (Adriatic Sea), denser sponge aggregations were found on rocks and dead corals than in areas with heavy sedimentation rates (Bo et al., 2011). In Halibut Channel, Haddock Channel, Desbarres Canyon, and The Gully (eastern Canada margin), observed species combinations were dependent on the dominant substrate type (Hargrave et al., 2004; Mortensen and Buhl-Mortensen, 2005; Baker et al., 2011). Sponge diversity was also positively correlated with substrate heterogeneity in five canyons off the southeastern Australian margin (Schlacher et al., 2007).

Structure-forming corals can occur in dense patches, fields or reefs in canyons. Coral colonies can form mound-like features (bioherms) or are found attached to vertical walls, overhangs, drop stones, or any exposed hard substrata within canyons (Orejas et al., 2009; De Mol et al., 2011; Huvenne et al., 2011;

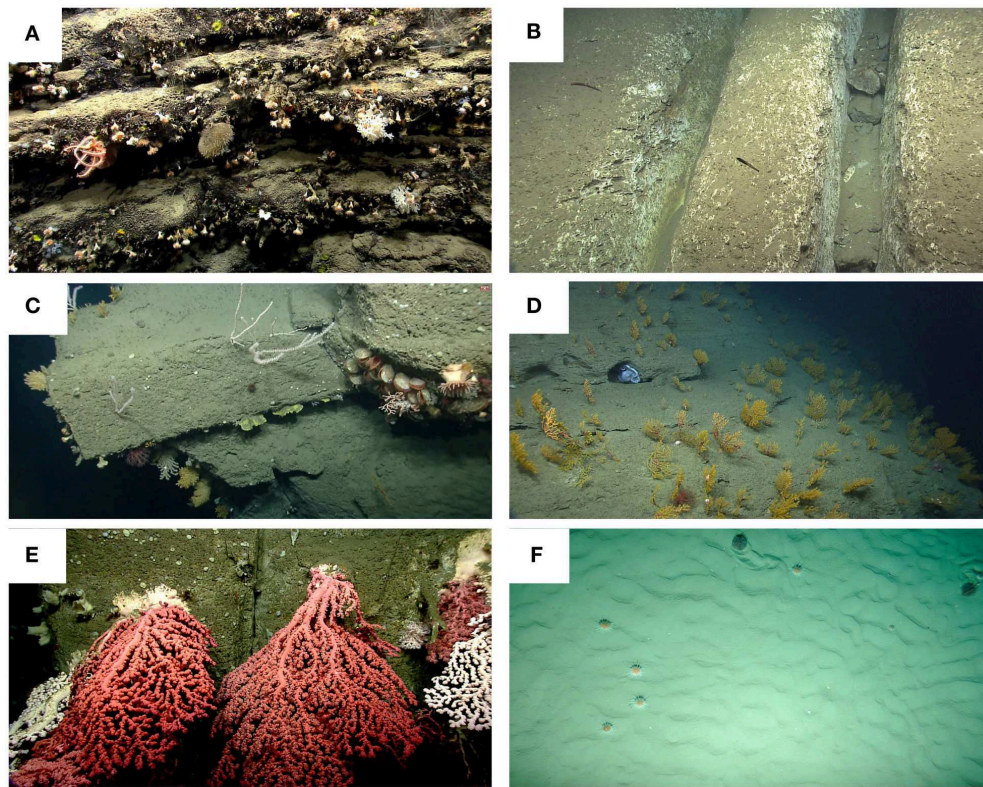


FIGURE 2 | Examples of substrate types in submarine canyons. (A) Stony corals (predominately the solitary coral, *Desmophyllum dianthus*), sponges and a brisingid sea star populate the rugged, manganese-encrusted rock ledges observed on the wall of Nygren Canyon. **(B)** Chutes, pictured here in Lydonia Canyon, are formed by physical abrasion of the carbonate-rich rock. **(C)** A variety of coral species and limid bivalves colonize the edges and smooth faces of tabular blocks and eroded mudstone and siltstone in Oceanographer Canyon. **(D)** An extensive field of *Paramuricea* sp., most hosting associated invertebrates, blankets the side of Welker Canyon. Note the octopus (center photo) sheltering in a small cave. An orange, rubber work glove partially buried on the floor of an un-named minor canyon adjacent to Shallop Canyon. **(E)** Numerous, large colonies of *Paragorgia arborea* were observed on the walls of Heezen Canyon. Corals, some as large as 5 m, attached to steep, clean walls, grow into the canyon channel. Photo credit **(A–E)**, NOAA *Okeanos Explorer* Program, 2013 Northeast U.S. Canyons Expedition. **(F)** Two unidentified echinoid species on soft sediment in a Bay of Biscay canyon (NE Atlantic). Copyright: Ifremer, Evhoe 2010.

Davies et al., 2014; Sánchez et al., 2014). However, patches or reefs, particularly those composed of scleractinians, often have a low density of live corals and a high amount of sediment between the colonies. In canyons, the ecosystem engineering role of cold-water corals and sponge fields has not yet been studied in detail, which contrasts with the significant data available for carbonate mounds and seamounts on the role of corals as autogenic engineers providing substrate, shelter and/or feeding place for associated species (Buhl-Mortensen et al., 2010; Santos et al., 2010). Nevertheless, there are several examples of fish and invertebrate associations with corals in canyons. In the Bering Sea, rockfishes, sculpins, poachers, and pleuronectid flounders are associated with high densities of gorgonians, pennatulids, and sponges in Zhemchug and Pribilof canyons (Miller et al., 2012). In The Gully (NW Atlantic), Mortensen and Buhl-Mortensen (2005) found a positive relationship between coral species richness and the total number of megafauna taxa, however, the abundance of fish was not correlated with the abundance of corals. Coral species richness was an important factor in explaining the variation in both fish and crustacean

assemblages in northwestern Atlantic canyons (Quattrini et al., 2015). Tissot et al. (2006) hypothesized that sea pen fields on deep banks off California (E Pacific) may have an important role as refuges for small invertebrates. In the canyons off Newfoundland, however, sea pen fields did not noticeably enhance the densities and richness of megafaunal assemblages (Baker et al., 2011).

Sediment instabilities and turbidity flows give rise to disturbance regimes in canyons that can affect the dynamics of some benthic populations and communities. For example, episodic disturbance events, caused erosive flows, and sediment-mixing processes linked to current modifications induced by the canyon topography, contribute to the instability of sediments, making conditions unfavorable to many infaunal species (Romano et al., 2013). As a consequence, differences in life-history strategies are reflected in species composition of the infaunal assemblages (e.g., nematodes) in different habitat types, with, for example, opportunistic species being more abundant inside canyon systems (Gambi and Danovaro, 2016). Sediment removal from the shallower canyon regions toward the deeper margin areas can also cause a decrease in overall available

nutritional material. This decrease in food availability can lead to a progressive decrease in local abundances of benthic and demersal fauna, with a subsequent decline in overall biodiversity (Pusceddu et al., 2013). Benthic communities may experience periodic cycles of disturbance, recolonization and eventual recovery of communities (McClain and Schlacher, 2015). For example, Hess et al. (2005) studied benthic foraminifera contained in a time series of samples taken in Capbreton Canyon (Bay of Biscay, NE Atlantic) after a down-slope turbidity flow event. Their results suggest that populations of foraminiferans recovered in about 6–9 months. Samples taken down-core in successive turbidity sequences contained nearly the same faunal elements as the surface assemblages. Thus, it appears that community structure of these benthic foraminifera is confined to an early stage of recolonization (Hess et al., 2005). In Nazaré Canyon (off Portugal), Paterson et al. (2011) found that frequent physical disturbance in the middle and upper sections of the canyon axis had a dramatic impact on foraminifera, with only certain species able to colonize and survive in these habitats. These two studies are testament to the influence that relatively high frequency (sub-annual) turbidity currents can have on determining benthic community structure in canyons.

CANYONS AS PROVIDERS OF ECOSYSTEM SERVICES

The Millennium Ecosystem Assessment (MA, 2005) identified the conservation of ecosystems and their environmentally-sustainable use as priorities to ensure the long-term well-being of the planet. To this end, understanding ecosystem services is essential. Ecosystem goods and services (hereafter, just services) refers to the socio-economic concept that places high regard on the benefits derived from ecosystem services that sustainably support human wellbeing (Armstrong et al., 2012; Thurber et al., 2014). Consequently, the focus of conservation has shifted from the conservation and preservation of species for the sake of the species only, to the conservation of the benefits derived from ecosystem services (MA, 2005). Ecosystem services can be classified into four major categories: (1) supporting services: those functions that feed into the other services, (2) provisioning services: goods obtained directly from habitats and ecosystems, (3) regulating services: benefits obtained through the natural regulation of habitats and associated ecosystem processes, and (4) cultural services: societal benefits, for example in terms of aesthetics and education (reviewed in Armstrong et al., 2012).

Supporting Services

Supporting services have an indirect effect, both physically and temporally, on human wellbeing, as they include the ecosystem functions (e.g., nutrient cycling, habitat provision, water circulation, or resilience) on which the other services are based (Armstrong et al., 2012). Submarine canyons provide several supporting services, through their role in sustaining marine food webs (van Oevelen et al., 2011) and providing a variety of habitats, including areas for larval settlement and

recruitment (Sardà and Cartes, 1994; Fernandez-Arcaya et al., 2013). Canyons facilitate the transport of nutrients from the shelf to the deep basins, affecting the overall faunal abundance and biodiversity of an area (see Section The Ecological Role of Canyons), and play a role in the maintenance of provisioning services within canyons (e.g., fisheries, see Section Provisioning Services). The role of canyons as nursery and refuge grounds is important in maintaining these provisioning services. For example, populations of the red shrimp *Aristeus antennatus* in NW Mediterranean canyons undergo seasonal ontogenic migrations closely related to the geomorphology of the canyons (Sardà et al., 2009). Company et al. (2008) suggest that the large augment of nutrients transported during cyclic dense shelf-water cascading events provide an increased food resource that enhances recruitment of *A. antennatus*. The authors suggest that these cyclic natural events help mitigate the general increasing overexploitation trend of this species observed over the last six decades. The red-shrimp fishery is extremely important for the Fishermen's Guilds in the NE Spain region. In 2014, the red-shrimp fishery generated over 14 million of Euros for Catalonia alone (Unpubl. data. Directorate of Fishing and Maritime Affairs, Government of Catalonia, Barcelona, Spain.). **Figure 3** shows the relationship between *A. antennatus* catches and the presence of submarine canyons, providing evidence of the supporting services offered by submarine canyons.

Regulating Services

Regulating services refer to benefits provided by natural regulatory functions of ecosystems through processes such as climate regulation, carbon sequestration, or detoxification of waste (Armstrong et al., 2012). Canyons play an important role in regulating carbon storage (Canals et al., 2006; Masson et al., 2010) and waste detoxification (Jobstvogt et al., 2014). As conduits for transport of sediment and organic matter to the deep sea, canyons contribute to the burying of carbon by taking it away from the surface layers and hence, play a role in climate regulation. Typically, biogenic particles settling on the seafloor undergo cycles of transport and re-deposition, influenced by tidal, storm, and cascading currents (de Stigter et al., 2011; Palanques et al., 2012; Sanchez-Vidal et al., 2012). Eventually, these particles reach a permanent accumulation region in zones of low hydrodynamic energy (de Haas et al., 2002). In canyons, specific hydrodynamic processes and higher particulate transport result in a significant cycling of organic carbon. This nutrient cycling service plays an important role in the gas, climate and waste regulation function, which in turn influences human health and productivity (De Groot et al., 2002). Additionally, these same transport processes can remove pollutants from shelf areas, carrying them to the deep sea where they are buried, transformed, or assimilated through processes such as bioturbation, decomposition, and sequestration (Armstrong et al., 2012). The monetary value of these services is currently outside the market system, with the exception of gas regulation (\$1.3 10^9 /year) (Costanza et al., 1997, 2014). Thus, the full monetary benefits of these regulating services have yet to be evaluated for canyon systems.

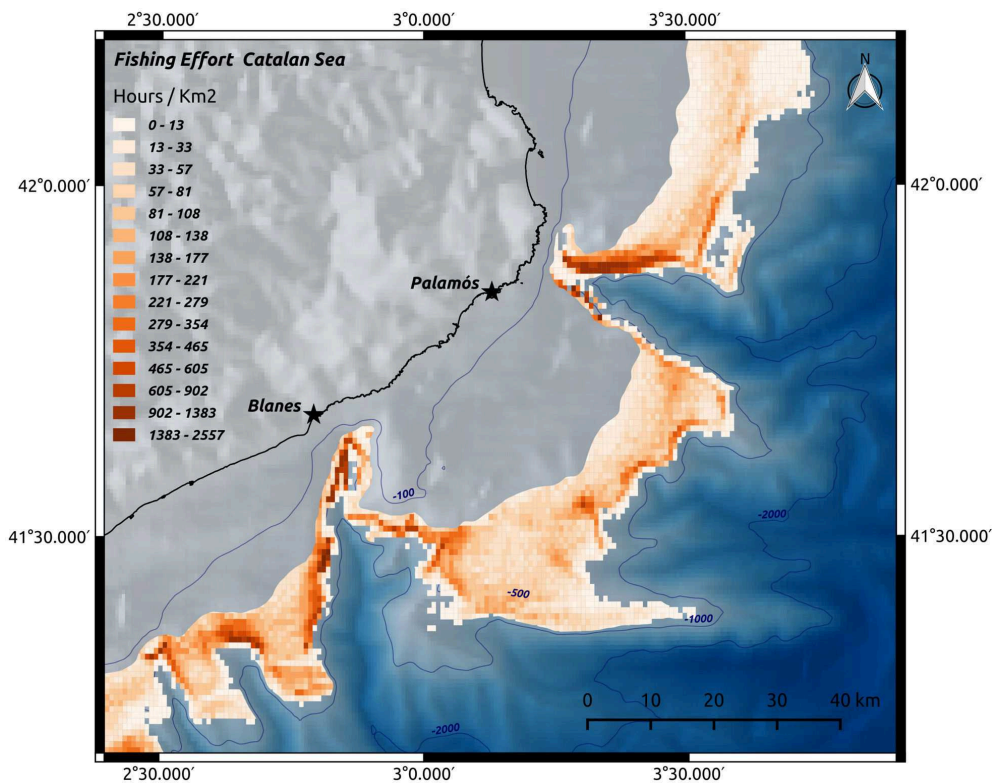


FIGURE 3 | Spatial overlays of *A. antennatus* catch per unit effort (by trap fishery) on the bathymetric surface. High values are spatially associated with canyons. The trawling activity has been obtained by Vessel Monitoring System data from DeepMed Research Group[®]. (2006). (Biological data collection).

Provisioning Services

Provisioning services refer to the products obtained directly from the ecosystem, such as fish, hydrocarbons, minerals, or genetic resources. Submarine canyons can directly provide food resources through exploitation of the fish stocks and other species (e.g., crustaceans) occurring within them. However, most fisheries take place on the slopes adjacent to the canyons, where fishing is easier. In these cases, canyons can provide supporting services in the form of habitat, food, and nursery areas for commercial species (see Section Supporting services). Another provisional service of submarine canyons is as a source for cold-water corals harvested for jewelry (Foley and Armstrong, 2010). Canyons can also be a source of genetic resources. The deep sea is a particular target for biodiscovery because specific conditions (e.g., total darkness, low temperature, high pressure, and in some cases such as hydrothermal vents, very strong thermal gradients, and high concentration of metals) result in specific physiological and cellular adaptations of the fauna. These adaptations increase the likelihood of finding unique secondary metabolites that can be highly useful for commercial production of medicinally important compounds. The high “hit” rate in recent bio-discovery studies in the deep sea supports this prediction (Skropeta and Wei, 2014). Since the 1990s, almost 80% of novel marine natural products from invertebrates were derived from cnidarians and sponges (ca. 90% of the cnidarian discoveries being from octocorals; Leal et al., 2012). In

a review of marine natural products, Blunt et al. (2013) emphasize that discovery of new marine-derived bioactive compounds are predominately from sponges. However, the importance of cnidarians as a source of these compounds is increasing, with an enormous unexploited resource yet to be explored (Blunt et al., 2013). Deep-sea canyons are a potentially rich source of genetic resources because they have high abundances of cnidarians and sponges (see Section Canyon effects on benthic sessile fauna and infauna). Finally, the potential monetary benefits of offshore drilling for hydrocarbons are large. Although this industry has not yet developed in submarine canyons, the oil and gas industry has started to explore options for development in these areas (see Section Oil and gas exploitation for more details).

Cultural Services

Cultural services are non-material benefits provided by the esthetic, educational, scientific, artistic, and recreational aspects of the ecosystem (Armstrong et al., 2012; Thurber et al., 2014). As part of the deep sea, the remoteness of submarine canyons and our relatively limited knowledge of their faunal communities greatly increase their interest and fascination. The mysteries largely hidden in the deep ocean fuel the imagination of civil society, including artists and scientists. Considerable amounts of funding are being invested in research to increase the understanding of canyon systems and their ecological function, followed by the promotion of awareness to promote canyon

stewardship (Strang and Tran, 2010; Thurber et al., 2014). In the last 10 years, several national and international science projects fully or partially focusing on submarine canyons have been funded (e.g., the HERMES and HERMIONE projects were supported with 15.5 M euro and 8 M euro, respectively, by the European Commission seventh Framework Programme (FP7). Fascination with the deep-sea realm is not recent, as shown by the internationally renowned adventures aboard the submarine *Nautilus* in *Twenty Thousand Leagues Under the Sea* by Jules Verne (1870). However, current technology provides opportunities for civil society to explore, remotely, regions of the planet that were not accessible to most people until recently. Cabled observatories, such as Ocean Network Canada's in Barkley Canyon, provide a window for the public into the deep sea by offering online, real-time views of the canyon seabed. Similarly, ROV cruises with real-time video streaming online (e.g., as provided by NOAA Office of Exploration and Research and the Ocean Exploration Trust), help to provide this cultural service to a wide public. Through films (e.g., Blue Planet series, BBC), books (e.g., *Deeper than Light* by Baker et al., 2011, *The Deep* by Claire Nouvian), exhibitions (e.g., *Deeper than Light* produced by the MAR-ECO and other deep-sea Census of Marine Life projects; *The Deep*, produced by C. Nouvian), and online platforms (e.g., Oceans Network Canada—Learning; telepresence-coverage of expeditions on NOAA ship *Okeanos Explorer*), it is possible for many people to gain a better understanding and appreciation of the deep sea, with its fascinating habitats and life forms. Other “cultural” services, although not available in all canyons, are whale-watching tourism (e.g., Kaikoura Canyon, off New Zealand) and surfing competitions (Nazaré Canyon, off Portugal). The increase in awareness about the deep sea and canyon ecosystems, including their value and the current and potential impacts they face, will likely result in an increased and significant social demand for management and conservation measures. Attempts have been made to assess public perceptions of the value of deep-sea ecosystems. A choice experiment showed that the Irish public would be willing to endorse a trawling ban in all areas where corals are thought to exist, and pay a personal tax of 1 euro per year in order to protect these habitats (Wattage et al., 2011).

HUMAN ACTIVITIES IMPACTING CANYON ECOSYSTEMS

Five major sources of impacts are threatening submarine canyon ecosystems: fishing; oil and gas exploration and exploitation; pollution, including marine litter, chemical pollution, and submarine disposal of tailings produced by land-mine activities; ocean acidification; and climate change-related stressors (Levin and Le Bris, 2015).

Direct and Indirect Effects of Fishing

Among the human activities that can severely impact the deep-sea floor and associated biological communities, bottom trawling is arguably one of the main concerns, because of its physical impact, geographical extension, and recurrence (e.g., Jones, 1992;

Benn et al., 2010; Ramirez-Llodra et al., 2011; Puig et al., 2012; Clark et al., 2015). Submarine canyons are not an exception and the enhanced presence of marine life in and around some canyons results in these ecosystems increasingly being targeted by commercial fisheries, including bottom trawling and dredging. As part of the general offshore expansion of bottom-trawling fleets during the last decades, the rims of submarine canyons, from the shelf edge down to mid-slope depths, have been increasingly targeted (Martín et al., 2014b). Large quantities of orange roughy (*Hoplostethus atlanticus*), black scabbardfish (*Aphanopus carbo*), oreos (e.g., *Pseudocyttus maculatus*) and various macrourid (e.g., *Coryphaenoides rupestris*) species have been exploited from deep-sea habitats. Deep-sea fishes tend to have intrinsically low growth rates and low fecundity, meaning that sustainable exploitation requires a very low catch rate (Norse et al., 2012; Clark et al., 2014). Furthermore, there is evidence that fishing in these ecosystems may cause substantial damage to the fragile, long-lived, sessile fauna such as structure-forming corals (Foley et al., 2011) and sponges. As a consequence, this exploitation has been compared to mining activities, because the resource is considered non-renewable on the scale of reasonable human lifespan (e.g., Clark et al., 2010; Armstrong et al., 2012).

In the NW Mediterranean Sea, an intensive fishery targeting the red shrimp *Aristeus antennatus*, has taken place for over six decades along the upper slope and around the deeply incised local canyons on the margin (Tobar and Sardà, 1987). The decrease of the yield per recruit, CPUE (catch per unit effort) and mean individual length over the last 20 years is probably a symptom of population changes induced by the intense exploitation (Gorelli et al., 2016). In addition to the impact on the biological communities, studies conducted in this area, within La Fonera (or Palamós) Canyon, have revealed that the trawling gear passing near and along the canyon flanks down to 800 m depth significantly impacts the seafloor (Puig et al., 2012). Trawl gear produces extensive sediment resuspension (Figure 4), erosion, organic carbon impoverishment, and ultimately, results in enduring changes to seafloor morphology at the spatial scale of the entire continental margin (Puig et al., 2012; Martín et al., 2014a). Sañé et al. (2013) identified a loss in the bioavailable content of organic matter, mainly amino acids, along the trawled flanks of La Fonera Canyon, while Pusceddu et al. (2014) documented notable ecological consequences of intensive trawling. These authors found that trawling, by continuously stirring the soft sediment of seabed over the years, has led to an 80% decrease in abundance and 50% reduction in the biodiversity of meiofauna. Additionally, nematode species richness decreased by 25%, when compared to similar areas where no trawling occurs. Data also revealed that trawled sediments are impoverished (over 50% reduction) in organic matter content and have lower rates of carbon degradation (about 40%). These results suggest that continued deep-sea trawling represents a global threat to seafloor biodiversity and ecological health of submarine canyons, causing effects on their flanks similar to those resulting from agricultural plowing and human-accelerated soil erosion on land (Puig et al., 2012; Pusceddu et al., 2014). Moreover, the impacts of trawling-induced resuspension of sediments are not restricted

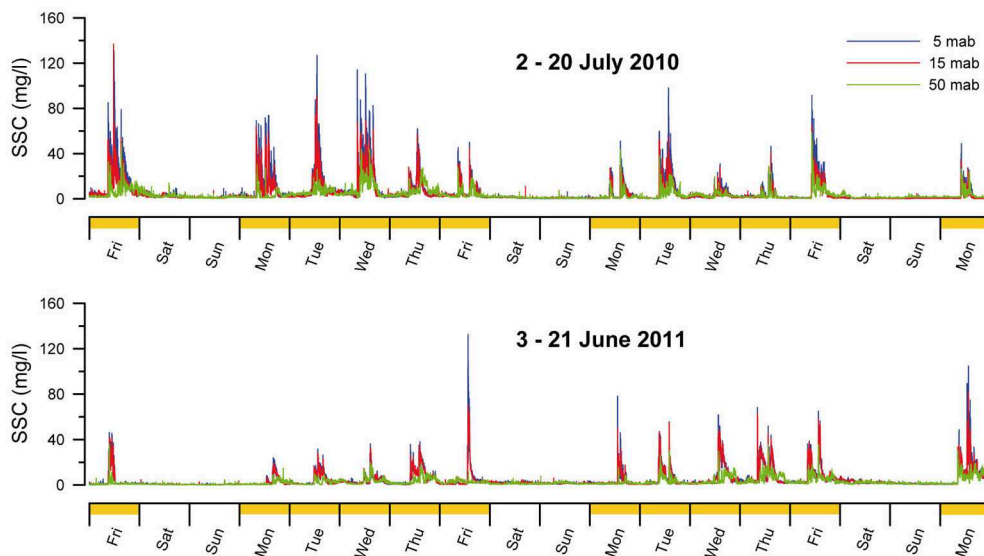


FIGURE 4 | Time series observations of trawling-induced resuspension events recorded at the northern flank of La Fonera Canyon during two different years. Note that suspended sediment concentration (SSC) peaks measured at different heights above the sea floor (mab: meters above bottom) were observed during weekdays (that is, working days for the fishing fleet illustrated as orange bars on the x axes), but not on weekends. Plots created from data reported in Puig et al. (2012) and Martín et al. (2014c).

to fishing grounds, since re-suspended sediments are advected from trawled areas toward greater depths, concentrated within nepheloid layers, and deposited into canyons through sediment-laden density flows triggered by trawling gear along steep canyon flanks (Palanques et al., 2006; Puig et al., 2012; Martín et al., 2014c). Martín et al. (2008) through radionuclide dating of a sediment core collected at 1750 m depth in the axis of La Fonera Canyon (NW Mediterranean), documented a doubling of the sediment accumulation rate in the 1970s, coincident with the rapid industrialization of the local trawling fleet. Puig et al. (2015) revisited the same canyon area a decade later and confirmed the two fold increase in the sedimentation rates during the 1970s, but also suggest that the accumulation rate during the last decade could be greater than expected, approaching $\sim 2.4 \text{ cm y}^{-1}$ (compared to $\sim 0.25 \text{ cm y}^{-1}$ pre-1970s). No submarine canyon in the world has been studied as intensively as La Fonera Canyon for the effects of bottom fishing gear, but given that canyons are often targeted by fisheries, it is likely that similar and other impacts have occurred and are occurring in other canyons elsewhere in the world. In Whittard Canyon (NE Atlantic), unusual peaks in nepheloid layers with much higher concentrations of suspended particulate matter ($\sim 1\text{--}8 \text{ mg L}^{-1}$) than normal ($\sim 0.075\text{--}0.5 \text{ mg L}^{-1}$) have been observed (Wilson et al., 2015b). Using VMS (Vessel Monitoring System) data from fishing vessels at Whittard Canyon, these peaks were linked to trawling activity (Wilson et al., 2015a). The direct and indirect impacts of trawling can affect cold-water corals and sponge fields. These two taxonomic groups are considered highly vulnerable, because they are usually slow-growing (up to 4–10 mm a year; e.g., Roberts, 2009 and references herein), long-lived and sessile, and thus very fragile and easily

disturbed. Vulnerable Marine Ecosystems (VMEs), such as coral (e.g., *L. pertusa*) reefs and deep-sea sponge aggregations that can occur in canyons, are recognized as habitats in need of protective measures by several international organizations (e.g., OSPAR, ICES, and FAO). For VMEs threatened by trawling on continental slopes, the complex morphology of canyons might offer the last refuge (Huvenne et al., 2011). Fabri et al. (2014), for example, suggested that in the NW Mediterranean Sea, most current dense aggregations of the gorgonian *Isidella elongata* occur on the steep slopes of canyons unreachable to trawling. However, the full extent of the impact of trawling gear on non-target benthic fauna such as corals is unknown. Although baseline ecological data of the “pristine” ecosystem is often not available, long-term studies of certain areas and landing and discards data from fisheries provide information on the changes taking place in benthic communities. For example, Company et al. (2012) suggest that there is a canyon effect on the community structure of the benthic megafauna of Blanes Canyon (NW Mediterranean), but that differing fishing pressures targeting the red shrimp *A. antennatus* on the margin and in the canyon may modulate the observed patterns. Trawling effects are also implicated in inducing changes to the trophic structure of benthic communities. The results of a comparative study of the benthic community on two margins (including canyons) affected by differing fishing pressures showed a predominance of mobile-predator scavengers and decrease of suspension-, filter-, and deposit-feeders in the areas of higher trawling intensity, compared with other areas where the trawling intensity was lower (Bowden et al., 2016).

Longline fisheries also occur in canyon systems (e.g., sablefish *Anoplopoma fimbria* and groupers *Epinephelus* sp). Although this

gear does not cause as much damage as trawling, when placed over coral habitats, the line can become entangled with the coral thus damaging the colonies during gear recovery (Orejas et al., 2009; Fabri et al., 2014). Additionally, ghost fishing is a well-reported problem related to lost gillnets or traps which continue to catch fish and damage other species.

Oil and Gas Exploitation

Submarine canyons coincide with some areas targeted by the offshore oil and gas industry for exploration and development opportunities. Examples include potential economic deposits located off West Africa (Jobe et al., 2011) and the Campos Basin located on the continental slope of Brazil, which is currently under production by PETROBRAS and other companies (Gorini et al., 1998; Day, 2002). In Australia, an assessment was made by Harris et al. (2007) of the seafloor features most characteristic of offshore oil and gas leases. Surprisingly, nearly 24% of Australian submarine canyons occur in oil and gas leases even though such leases cover only 8.7% of Australia's EEZ (Exclusive Economic Zone). Thus, it would appear that, at least for Australia, submarine canyon habitats are positively selected for with regard to oil and gas leases, in comparison to other seafloor geomorphic features.

Over the last 10 years, several studies have focused on the effects of exploratory offshore drilling in response to the growing interest by the oil and gas industry to move operations further offshore (Currie and Isaacs, 2005; Ellis et al., 2012; Bakke et al., 2013; Paine et al., 2014). This offshore shift is especially true for countries such as the United Kingdom, Norway, Italy, Malaysia, Indonesia, and Australia, which number among the leading oil-producing countries (Patin, 1999). Results from these and previous studies suggest that discharge of drilling waste is the primary environmental concern of oil and gas drilling operations. Drilling discharges are composed primarily of dense particulate solids that settle rapidly and accumulate in sediments down-current from the platform (Bakke et al., 2013). The rapid accumulation of these solids in the sediments has caused changes in benthic community composition (loss of rare species and increase in abundance of pollution tolerant species), decrease in abundances and diversity of communities and decrease in coral coverage among others (reviewed in Ellis et al., 2012). The effects of drilling discharge can also affect the biology, particularly growth and reproduction, of megafaunal species. For example, bentonite and barite particles may cause changes in reproduction and growth of scallops (Cranford, 1995). However, other studies indicate that the effects of elements incorporated in discharge are mainly a physical stress, while chemical toxicity is not always described (Bakke et al., 2013). Although studies specific to submarine canyons have not been conducted, the effects of drilling waste on benthic and demersal species is highly dependent on a number of local environmental variables (e.g., depth, current, and wave regimes, substrate type; Ellis et al., 2012). Thus, it is expected that similar or even greater effects in canyons because of the presence of VMEs (e.g., coral reefs) and potentially restricted movement of pollutants due to current regimes in canyons. Experimental and monitoring studies based on the exposure of *L. pertusa* to drill cuttings from oil drilling

activities on the Norwegian continental shelf indicate that corals polyps tolerate well the enhanced particle deposition rates and suspended matter concentrations (Allers et al., 2013; Larsson et al., 2013; Purser, 2015). However, a small pilot experiment indicated that coral larvae might be particularly vulnerable to high particle concentrations (Larsson et al., 2013). The effect of accidental oil spills from deep offshore drilling (e.g., Deepwater Horizon oil spill in the Gulf of Mexico, White et al., 2012) could also be more severe given the physical and hydrodynamic nature of submarine canyons.

Canyons As Sinks for Marine Litter and Chemical Pollution

The London Convention (1972) and London Protocol (1996) legally banned the dumping of litter from ships. However, litter occurs in all marine habitats, from the intertidal to abyssal plains, entering the marine system from the coast (rivers, beaches) and through illegal dumping (Galgani et al., 2000; Ramirez-Llodra et al., 2011; Bergmann et al., 2015). Although dedicated and opportunistic studies on deep-sea marine litter have increased in the last decade, knowledge is still sparse. However, the data obtained to date from regional, as well as international, large-scale investigations, suggest that canyons are a major habitat for the accumulation of litter (Figure 5). The specific hydrographic patterns and increased downslope currents in submarine canyons result in canyons becoming hotspots of marine litter (Galgani et al., 1996, 2010; Mordecai et al., 2011; Ramirez-Llodra et al., 2013; Schlining et al., 2013; Pham et al., 2014; Bergmann et al., 2015; Tubau et al., 2015; Van den Beld et al., in press). A study comparing the accumulation of marine litter in different deep-sea habitats across Europe showed that litter densities in canyons were higher than in other physiographic settings, such as continental shelves, seamounts, banks, and mounds (Pham et al., 2014). In the Mediterranean, a study of marine litter on the slope, deep basin and canyons indicated that canyons preferentially accumulate light debris (e.g., plastic), which is transported downslope from the shelf in highly populated coastal regions (Ramirez-Llodra et al., 2013). In Monterey Canyon (E Pacific), heavier litter tends to accumulate in high-relief outcrops or depressions, while soft plastics accumulate in areas where structure-forming corals provide relief on the seafloor (Figure 5, Schlining et al., 2013; Van den Beld et al., in press). The effects of litter on the benthic fauna are little understood. However, impacts such as suffocation, physical damage of sessile fauna (e.g., corals, sponges, crinoids) and ghost fishing from discarded or lost fishing gear have been observed (Ramirez-Llodra et al., 2013; Pham et al., 2014; Bergmann et al., 2015). The degradation of plastics into microplastics and their transport in the water column and accumulation in the sediments provides an additional source of concern (Thompson et al., 2009; Bergmann et al., 2015). These microplastics are potential sources of toxic substances (e.g., persistent organic pollutants) and if ingested, may have lethal or sub-lethal effects on the fauna as well as pose a threat to human health through their bio-accumulation in the marine food web (Thompson et al., 2009; Lusher, 2015; Rochman, 2015).

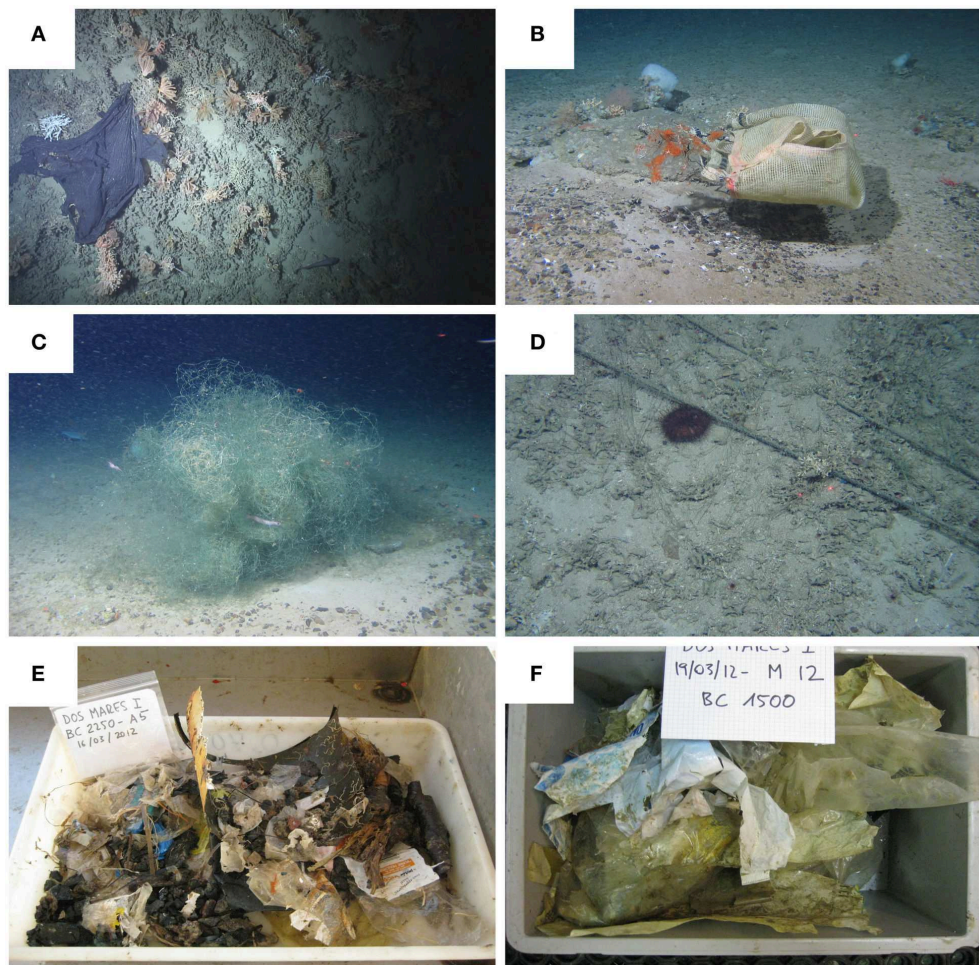


FIGURE 5 | Images of marine litter found in different submarine canyons. (A) A plastic sheet in a cold-water coral community in a Bay of Biscay canyon. Copyright: Ifremer, BobEco cruise 2011. **(B)** Coral damaged by trawling and trawl lines in unnamed northern canyon at 700 m. CE1004 cruise. **(C)** Remains of fishing gear over corals and other benthic fauna on Porcupine Bank. **(D)** Remains of longlines in an unnamed canyon north of the Porcupine Bank approx 1400 m (NE Atlantic). CE13008 cruise. Copyright NUI Galway / Marine Institute. **(E,F)** Examples of marine litter collected at Blanes submarine canyon (NW Mediterranean) at 2250 m **(E)** and 1500 m **(F)**, respectively. Copyright: ICM-CSIC, DOSMARES cruise 2013.

Investigation of chemical contamination of deep-sea ecosystems is increasing. Results show that chemicals are accumulating in deep-sea sediments, benthos, and mid-water fauna (Asante et al., 2008). The major contaminants of concern are persistent organic pollutants (POPs), toxic metals (e.g., Hg, Cd, Pb, Ni, and isotopic tracers), radioelements, pesticides, herbicides, and pharmaceuticals. The hydrodynamics of canyons favor the quick movement of labile material to the lower slope, where local benthic environments might become sinks of pollutants (Puig et al., 1999; Looser et al., 2000; Palanques et al., 2008; Castro-Jiménez et al., 2013; Cossa et al., 2014; Sanchez-Vidal et al., 2015). In the NW Mediterranean, general accumulation patterns indicate that organisms collected inside Blanes Canyon had higher concentrations of POPs than individuals collected on the adjacent open slope (Koenig et al., 2013). These inputs could be the consequence of enhanced vertical transport of hydrophobic particles associated with

chemical pollutants, the dispersal of which is driven by local hydrodynamic processes that regulate flux and sediment re-suspension patterns (Koenig et al., 2013).

Canyons as Areas for Mine Tailing Disposal

Land-based mining produces large volumes of waste in the form of non-processed overburden rock and processed fine particulate tailings. The tailings (fine-fraction slurry) usually account for a very high proportion of the ore (e.g., 99% for copper and 99.99% for gold, MMSD, 2002). Some tailings can, additionally, include process chemicals (e.g., floatation or flocculation chemicals) and heavy metals, and in some cases, very sharp particles resulting from the crushing process (Lake and Hinch, 1999). Although most mines use conventional land-based dams to store tailings, there is an increasing interest in submarine tailing disposal (STD), including deep-sea tailing placement (DSTP) (reviewed in Ramirez-Llodra et al., 2015). DSTP occurs where a pipe is

submerged below the mixing layer (>100 m depth), and where a turbidity flow is created that transports the tailings down to the deep seafloor. The environmental impacts of DSTP can include: (1) smothering of the benthic ecosystem in the deposition area through hyper-sedimentation; (2) chemical toxicity from metals or processing chemicals; (3) modified organic matter content and porosity of sediments (grain size and angularity) that can affect feeding and recolonization; (4) formation of sediment plumes and increased turbidity which may impact pelagic organisms; and (5) risk of slope failure and re-suspension of tailings (Ramirez-Llodra et al., 2015). Currently, seven mines across the world conduct DSTP, three in Papua New Guinea, one in Indonesia, one in France, one in Greece, and one in Turkey. When considering DSTP, canyons are often proposed as preferential locations because of their natural capacity to act as conduits to deep basins. For example, the Ramu Nickel Project in Papua New Guinea discharges tailings at 150 m into Basmuk Canyon, with a final deposition at 1500 m (Shimmield et al., 2010). The Indonesian Batu Hijau copper and gold mine has discharged its tailings at 125 m depth into Senunu Canyon since 2000, with final deposition between 3000 and 4000 m depth (Shimmield et al., 2010; Reichelt-Brushett, 2012). This DSTP is the deepest deposition of tailings in the world. In France, the alumina plants in the Marseilles area (NW Mediterranean) that process bauxite have discharged the red-mud residues produced by this process into Cassidaigne Canyon since 1967. The pipe is situated at 330 m depth and the red-mud deposit extends more than 50 km from the outflow into the abyssal plain (Dauvin, 2010; Fontanier et al., 2012; Fabri et al., 2014). Excess concentrations of iron, titanium, vanadium, and chromium are recorded on the seafloor (Fontanier et al., 2012). *In situ* observations of sessile fauna (e.g., gorgonians) covered by the red mud show signs of tissue necrosis, which indicate that there is a negative, or even lethal, effect of the accumulation of red mud on the megafauna (Fabri et al., 2014). Nevertheless, settlement of new coral colonies has also been observed, perhaps in response to the decrease in red-mud outflow since 1988, when one company stopped discharging tailings (Fabri et al., 2014).

GOVERNANCE AND MANAGEMENT OF SUBMARINE CANYONS

There is a range of legal and institutional frameworks for governing and implementing the conservation and sustainable use of marine systems. Despite the complexity of canyon management and conservation, in recent decades, some of these frameworks have been used to instigate conservation and management measures in different regions, and new frameworks are being proposed.

Legal Frameworks and Other Tools for Canyon Conservation

In 2008, the 9th meeting of the Conference of the Parties to the Convention on Biological Diversity (CBD, 2008, COP9) adopted seven scientific criteria for the identification of Ecologically or Biologically Significant Marine Areas (EBSAs) (annex I,

decision IX/20); these are, (1) uniqueness or rarity, (2) special importance for life-history stages of species, (3) importance for threatened, endangered or declining species and/or habitats, (4) vulnerability, fragility, sensitivity, or slow recovery of ecosystems, (5) biological productivity, (6) biological diversity and (7) naturalness. Under these criteria and based on the specific characteristics of canyons, the CBD suggested that submarine canyons could be classified as priority areas for conservation on many continental margins areas (Davies et al., 2014). Similarly, the United Nations Food and Agricultural Organization (FAO, 2009) adopted similar criteria to identify VMEs. The VME concept has gained prominence following a resolution of the United Nations General Assembly (UNGA, resolution.61/105) to seek the protection of VMEs on the high seas and in areas of national jurisdiction (Weaver et al., 2011). Examples of VMEs include canyon habitats, as well as the coral reef and sponge aggregations that are sometimes found in canyons (FAO, 2009). These two conservation initiatives, as well as other international initiatives, are providing a platform for Regional Fisheries Management Organizations (RFMOs), Regional Seas Conventions and Action Plans (RSCAPs), and other proposals developed in the past 10 years (Jobstvagt et al., 2014) to provide protection for species and habitats that are important for sustainable marine ecosystems. The aim is to strengthen cooperative work in the development of a common roadmap under the coordination of the United Nations Environment Program (UNEP-MAP-RAC/SPA, 2010). Canyon systems, by their association with continental margins, are more often found in EEZs, where the concepts of EBSAs and VMEs are neither always nor consistently applied by nation states. Nonetheless VMEs have been identified in canyons on the Mediterranean margin (Fabri et al., 2014). In Europe, the Oslo-Paris Convention (OSPAR) from 2005 provides a legal mechanism in the northeast Atlantic area to protect several deep-sea habitats, including those submarine canyon habitats where cold-water scleractinian reefs (i.e., dominated by *L. pertusa*) are present (OSPAR, 2005).

Most submarine canyons are located within (EEZs) (Huang et al., 2014), which gives individual nation states the authority to control all extractive activities in their area (e.g., fisheries, oil and gas), thereby these states potentially offer protection to canyons through conservation and management measures such as Marine Protected Areas (MPAs) or fisheries management tools such as spatial/temporal closures of areas or gear restrictions. However, international agreements concerning the rights of free navigation must also be acknowledged in the development of management measures that include such area-based protection regimes. The legal framework of marine environmental protection is complex given the different levels of legislation (international, national, and regional) and varies widely depending on the countries involved (Camuffo et al., 2011). The complexity of governance depends mainly on the canyon's location. In the case of a cross border location such as Capbreton Canyon (France/Spain, Bay of Biscay) or a large area of international waters such as in the Mediterranean region, the regional disparities in governance and institutional structures make it difficult to find agreements to ensure a sustainable management of ecosystems (De Juan et al., 2012). States have no mechanisms to create globally-recognized

MPAs and reserves on the high seas. Instead, there is a patchwork of bodies, including RFMO that set policies for specific areas of the ocean or specific activities (such as fishing for tuna). However, those bodies lack the legal mandate necessary to establish MPAs. Nevertheless, there are several examples of areas where progress has been made in the protection of canyon habitats (Table 1; Figure 6).

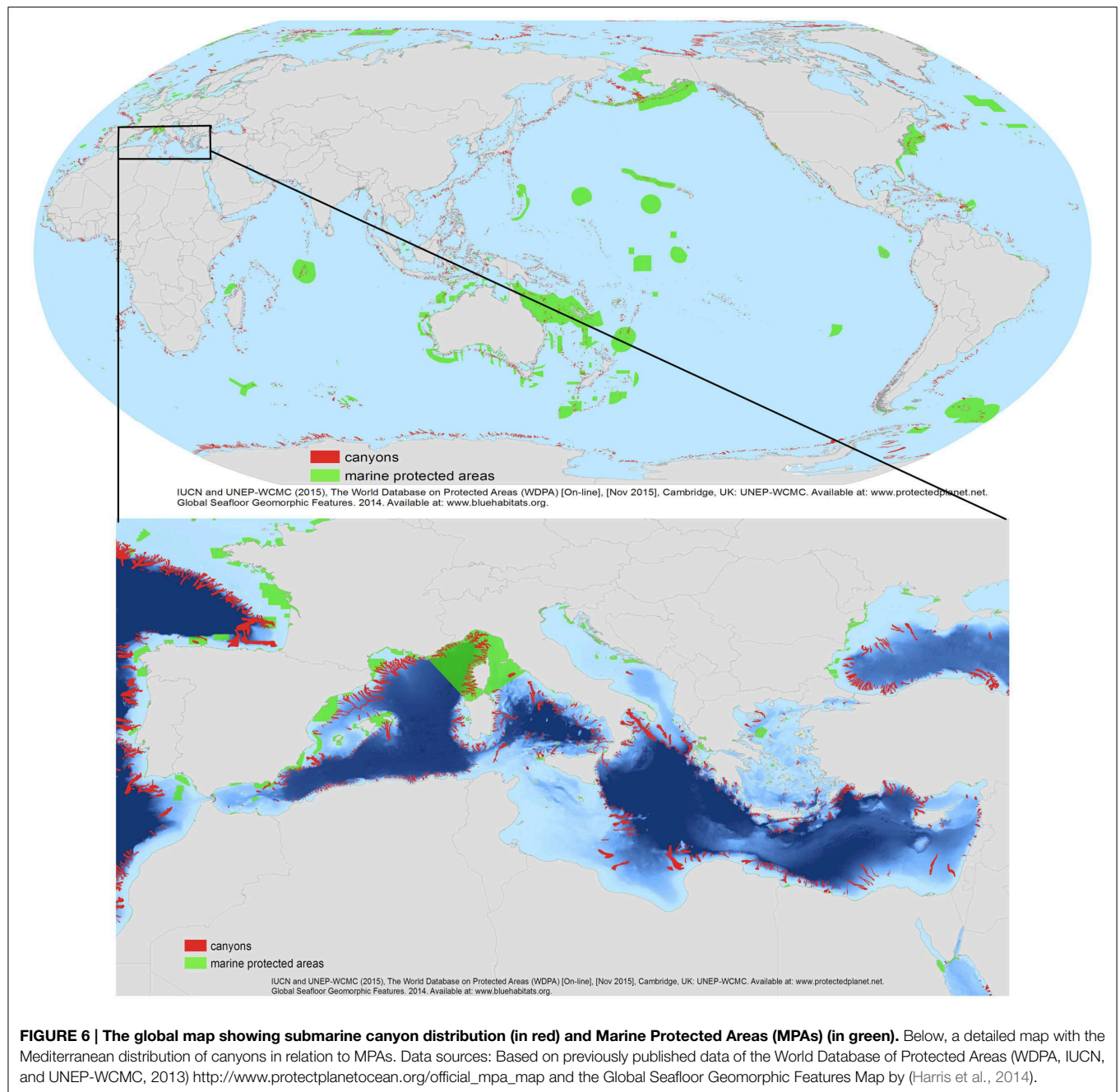
Examples of Current Canyon Conservation and Management

In Canada, The Gully MPA, located 200 km offshore Nova Scotia, was created in 2004 under Canada's Ocean Act. The Gully MPA, covering an area of 2364 km², includes three zones of protection based on conservation, management and research objectives (DFO, 2008; Westhead et al., 2012). The Gully Advisory Committee, composed of representatives from academics, industry and non-government organizations,

provides advice and information to the government on the MPA and related activities (DFO, 2008; Westhead et al., 2012). In the Northeastern United States of America (USA), in addition to a network of habitat closed areas implemented by Regional Fisheries Management Councils (RFMCs), the New England Fishery Management Council (NEFMC), and Mid-Atlantic Fishery Management Council (MAFMC), added two canyon habitat closures (Oceanographer and Lydonia canyons) within Amendment 2 of the Monkfish Fishery Management Plan. These closures were implemented as a precautionary approach to prevent impacts from the development of an offshore monkfish (*Lophius* sp.) fishery on Essential Fish Habitats (EFH) and deep-sea canyon habitats (Packer et al., 2007; Marin and Aguilar, 2012). Another example of fisheries management decisions benefiting preservation of canyon habitats is also in the western North Atlantic, off the east coast of the USA. Conservation measures designed to protect vulnerable marine species, such as deep-sea

TABLE 1 | Some examples of protected canyon initiatives and implement measures.

Submarine Canyon	Management	References
Capbreton Canyon (NE Atl)	Since 1985 designed as restricted fishing area (Ord. n°40 1985) for gillnets, and subsequent expansion to include restriction areas for pelagic and benthic trawlers	Sanchez et al., 2013
The Gully (NW Atl)	1992 Parks Canada selects the Gully as a Natural Area of Canadian Significance 1994 DFO establish the Gully as Whale Sanctuary Canadian Wildlife Service. MPA proposed in 1999 was accepted by the parties in 2004. The regulation make it illegal for any person to disturb, damage or destroy in the Gully MPA, or remove from it any living organism or any part of its habitats as well as depositing discharging or dumping of substances within MPA	DFO, 2008
Monterey Canyon (E Pacific)	Soquel Canyon State Marine Conservation Area and Portuguese Ledge State Marine Conservation Area was designated in 2007: It is unlawful to injure, damage, take, or possess any living, geological, or cultural marine resource, with the following specified exceptions: The commercial and recreational take of pelagic finfish is allowed	Online Guide to California's Central Coast Marine Protected Areas. 2008
Porcupine Bank Canyon (NE Atl)	Since 2009 designated as Special Area of Conservation (SAC) by Department of Arts, Heritage and the Gaeltacht (Ireland); the use of all bottom gears (including gillnets and longlines) are strictly forbidden	Guinan and Leahy, 2010
The Cassidaigne Canyon (Med)	Parc National des Calanques (decree 2012-507) included a "reinforced protection zone" and a "no-take zone" defined to protect CWC communities from fishing. The "reinforced protection zone" is a "no-take zone" with some exceptions for local artisanal fishermen.	Fabri et al., 2014
Canyons Marine Conservation Zone (NE Atl)	Designed in 2013 as Marine Conservation zone (MCZ). No fisheries management measures have yet been put in place to protect the designated features of this site but MMO are currently leading a work programme to identify appropriate management measures. As this site is offshore management measures will need to be proposed and agreed through the European Commission in accordance with the Common Fisheries Policy, applying to UK and non-UK fishing vessels alike.	http://jncc.defra.gov.uk/page-6556
Mid-Atlantic region (15 canyons)	Final approval is expected in late 2016. Under Magnuson-Stevens Fishery Conservation and Management Reauthorization Act (Public Law 109-479) all bottom-tending types of gear used in federally managed fisheries are prohibited in and around deep-sea coral habitat (i.e., canyons), with the exception of the deep-sea red crab trap fishery.	http://www.mafmc.org/actions/msb-am16



corals that occur in canyons provide a level of protection to the canyon as a whole. The MAFMC has approved the deep-sea corals amendment to protect known or likely coral habitat while limiting negative impacts to commercial fisheries operating in the region. Magnuson-Stevens Fishery Conservation and Management Reauthorization Act (Public Law 109–479) gives the RFMCs the authority to designate zones where, and periods when, fishing may be restricted in order to protect deep-sea corals from the impacts of fishing gear. The MAFMC considered various alternatives, and two spatially overlapping coral protection zones were selected as preferred options. The

broad coral zone prohibits fishing in regional waters at depths of 450 m and greater, out to the limit of the EEZ. Discrete coral zones define specific areas where corals are known to occur or are highly likely to occur based on results of a habitat suitability model. The boundaries of most discrete zones outline large portions of submarine canyons. Under this amendment, all bottom-tending types of gear used in federally managed fisheries are prohibited in and around deep-sea coral habitat (i.e., canyons), with the exception of the deep-sea red crab (*Chaceon quinque-dens*) trap fishery. This recent management recommendation in the western North Atlantic, if approved, will

protect approximately 99,000 km² of seafloor in the Mid-Atlantic region (East coast of the USA, Virginia to New York), including 15 canyons. Final approval is expected in late 2016. A similar situation can be found on the Eastern margin of the Atlantic, where Explorer and Dangeard canyons are part of a United Kingdom Marine Conservation Zone (MCZ). This conservation measure was put in place with the specific aim of protecting cold-water coral reefs, but as a result large parts of the canyons are protected.

In the Mediterranean Sea, effective governance of canyon systems requires cooperation at various levels, ranging from international conventions to regional initiatives for environmental protection (Cinnirella et al., 2014). The European Council has adopted management plans for specific Mediterranean fisheries, in areas totally or partially beyond the territorial seas (including high seas) and affecting canyon habitats. Such plans include the prohibition of fishing with trawl nets and dredges in certain areas, and at depths below 1000 m (EC Regulation 1967/2006). The Regional Activity Centre for Specially Protected Areas of Mediterranean Importance (SPAMI), under the Barcelona Convention agreements, has set up the legal framework to conserve marine habitats including submarine canyons (RAC/SPA, 2010). In the French part of the Mediterranean basin, three MPAs have been created to protect cold-water corals: the “Parc Marin du Golfe du Lion” (decree 2011-1269) including Lacaze-Duthiers, Pruvot and Bourcart canyons; the “Parc National des Calanques” (decree 2012-507) including Cassidaigne Canyon with specific regulations; and the “Parc National de Port-Cros” (decree 2012-649) with extension of the adjacent bathyal seafloor (Fabri et al., 2014, **Table 1**). In addition, the General Fisheries Commission for the Mediterranean (GFCM) established a fishing-restricted area off the French coast in the Gulf of Lion, including Montpellier, Petit-Rhône, and Grand-Rhône canyons in 2009 for the Mediterranean (Marin and Aguilar, 2012; Fabri et al., 2014). This directive involved the regulation of certain demersal fishing gears and aimed to protect spawning aggregations and deep-sea sensitive habitats (GFCM, directive no. 33/2009/1, IUCN and UNEP-WCMC, 2016). In Spain, Protected Areas, Marine Reserves and Marine Reserves of Fishing Interest have been established, but these protected areas include only a few submarine canyons.

In 2012, the International Union for Conservation of Nature (IUCN) published a book on Mediterranean submarine canyon ecology and governance (Wüertz, 2012), which was based on the conclusions of several workshops focusing on Mediterranean governance. It was recommended to Mediterranean countries that a precautionary principle be applied to the canyons under their jurisdiction, and to include canyons in national, regional and international strategies for MPAs. The increasing role of non-governmental organizations (NGOs) in calling for improvement in canyon management has resulted in investigations of the most vulnerable submarine canyons, and in some cases protection measures have been proposed (Marin and Aguilar, 2012). For example, in 2011, Oceana (i.e., nonprofit international organization focused solely on the protection of the oceans,

<http://eu.oceana.org/en/about-us>) published a new proposal for the protection of the Mediterranean vulnerable areas called MedNet. This proposal contained 28 submarine canyons (e.g., Bejaia Canyon, Algeria; Gulf of Lion submarine canyons, France and Spain; Bari Canyon, Italy amongst others) and included a detailed review of their main characteristics and current status of conservation initiatives (Marin and Aguilar, 2012). Some of these proposed canyons (e.g., Cap de Creus Canyon and Lacaze-Duthiers Canyon) have now been classified as Sites of Community Importance (SCI) under the EU Habitats Directive.

Although progress has been made to combine both marine conservation and fisheries management, it remains fragile due to disparities in regional governance and institutional structures between countries (De Juan et al., 2012). These authors highlight the complex jurisdictional situation of international waters in the Mediterranean Sea and mention the need for cooperation between coastal states with a regional operational strategy to achieve a sustainable management of ecosystems. The case of Capbreton canyon in the Bay of Biscay (NE Atlantic) provides an example of the difficulties that cooperation must overcome. Capbreton canyon extends from French territorial waters into the EEZ of both France and Spain, and is regulated through several management measures. In the French part, these measures were first established in 1985 (Ord. n°40 1985) at the request of local French fishermen and included fishing restricted areas for gillnets, and subsequent expansion to include restriction areas for pelagic and benthic trawlers (Sanchez et al., 2013). Most of the restricted area lies within the French Territorial Sea, but part extends into the French EEZ. The French restrictions in the EEZ area, however, do not apply to foreign vessels. The extension of such an area into the EEZ raises the questions of legality, enforcement, and monitoring for scientific purposes (Sanchez et al., 2013). Additionally, the cross border location between France and Spain of Capbreton Canyon makes fisheries management even more complicated, making agreements on trans-boundary cooperation difficult. Proposals for a management plan of a “Capbreton case study” were discussed between stakeholders during European project GEPETO (<http://gepetoproject.eu/>), which aimed to improve future fisheries management in the south European Atlantic coast region (Uriarte et al., 2014).

Global Submarine Canyon Protection Status

A recent review of global seafloor geomorphic features, based on the analysis and interpretation of a modified version of the SRTM30_PLUS global bathymetry grid (Becker et al., 2009), included a new assessment of submarine canyons and associated geomorphic statistics (Harris et al., 2014). The database that underpins the analysis of Harris et al. (2014) provides the information needed to estimate the area of canyons within each country's EEZ as well as the area of canyon currently protected within MPAs. Here, we provide an analysis using ArcGIS ESRI tools on the proportion of canyons included in MPAs at the global scale (**Figure 6; Table 1**). Statistics included the area estimates for

9477 individual canyons covering a total area of 4,393,650 km² (i.e., 1.2% of the total ocean area).

In order to estimate the area of canyons within EEZs (i.e., canyon area that can be protected within the jurisdiction of individual countries, as opposed to those located in the high seas or areas beyond national jurisdiction), global EEZ boundaries downloaded from the VLIZ database were used. In addition, a summary of global MPA boundaries was downloaded from the IUCN and UNEP-WCMC database (IUCN and UNEP-WCMC, 2016) and used to calculate the areas of canyons within MPAs. Results showed that of the overall 4,037,764.35 km² of seafloor found in submarine canyons in EEZs (91.9% of canyon area), 13.6% of canyon areas are protected (with at least 10% of their area) within an MPA. Only 10.3% of all canyons are completely protected (100% of their area) within an MPA (Table 2, Annex I).

This exercise identified 1956 canyons within MPAs (Table 2, Annex I). Of the 191 countries/jurisdiction with submarine canyon(s) in their waters, 163 countries (83% of the total) have less than 10% of their submarine canyon(s) protected within an MPA. Only 12 countries (6.3%) have 100% of their submarine canyons covered by MPA protection. From these last 12 countries/jurisdictions, 10 are overseas territories of France and the United Kingdom (e.g., British Indian Ocean, Glorioso Island, Ile Europe, see Annex for more detail) while the other two countries (i.e., Djibouti and the Democratic Republic of Congo) have protected the only canyon they have in their waters (Annex 1). In terms of numbers, the United States and New Zealand protected the highest number of canyons (117 and 54 respectively). Indonesia and the Philippines had the highest number of canyons within their EEZs (576 and 265 from which 20 and nine were protected respectively, Annex 1). Notably, these results only reflect those canyons protected by management provided under MPA authority. However, there are other mechanisms in place that offer other protective measures (i.e., world heritage area marine park and fisheries management areas). Yet, no standardized world database exists that includes

all protected canyon areas. Therefore, some level of worldwide synthesis, although difficult to achieve, is needed to assess the conservation actions undertaken for canyon protection. The data (see detailed Figure 6 of the Mediterranean Sea) also reveal that most of the marine conservation measurements have focused on shelf ecosystems, while the vast majority of continental slope areas around the world (where submarine canyons are found) are still without any regulations to prevent them from pollution and human exploitation.

DIRECTIONS FOR FUTURE CANYON RESEARCH

Progress in submarine canyon research has provided considerable evidence demonstrating that canyons are seascape that host important ecosystems, and are in need of conservation. However, there are still many important scientific questions and unknowns, which hamper the development of effective conservation and management strategies for these important ecosystems.

Knowledge Gaps and Future Directions for Understanding Canyon Ecosystem Functioning and Services

Although the broad-scale physical and geological patterns and processes in submarine canyons have now been identified (e.g., the occurrence of turbidity currents, dense shelf water cascading, internal waves), their fine-scale effects and distributions are less well understood (e.g., their frequency, exact footprint, or sediment types affected). However, it is often those finer scale effects that directly influence species and communities, and a better understanding of these will lead to more robust decisions about community vulnerability, which canyon areas to prioritize for protection, and how to interpret species resilience against different types of disturbance. Small-scale effects within canyons can also influence ecosystem services, and many questions remained unanswered about these influences. For example, what is the exact effect of sediment flows and repeated resuspension on the carbon cycle within submarine canyons (as an ecosystem service)? What role does canyon geomorphology play in the determination of biodiversity and ecosystem functioning? Overall, to achieve this better resolution in our understanding, more canyons need to be studied, studies need to be long term (time-series), and studies need to be better coordinated. There is a need for more baseline surveys, using standardized methodologies and the most appropriate sampling schemes (Ayma et al., 2016). Also in general, better integration is needed across the different disciplines of submarine canyon studies, combining insights from sediment dynamics, oceanography and biogeochemistry with biological knowledge, to achieve a more holistic understanding of submarine canyon systems (e.g., Amaro et al., 2016).

Recent development of new technologies offers exciting new opportunities to answer some of the questions posed above, and to better integrate fields of study. Although the rugged topography of canyons has often limited ecological

TABLE 2 | Summarizes the total number (N) of countries/jurisdiction with at least 100 and 10% of their canyon area within MPAs (for more details see Annex 1).

% of protected canyons	N of countries 10% of canyon within MPAs	N of countries 100% of canyon within MPAs
0–10	151	163
20–30	9	4
20–30	4	2
30–40	3	3
40–50	6	2
50–60	0	2
60–70	2	1
80–90	1	2
90–100	15	12
Total	191	191

research due to restrictions of traditional sampling gear (e.g., trawling, coring), underwater technologies such as Autonomous Underwater Vehicles (AUVs), ROVs, and cabled observatories are providing new and sophisticated platforms to observe, sample and experiment in submarine canyons. Benthic multiparametric platforms endowed for oceanographic, geologic, and chemical sensors allow remote investigation of the canyon environment. When these sensors are associated with imaging and acoustic equipment, species presence can be related to particular states in the monitored environmental variables providing important data on community temporal dynamics (Aguzzi et al., 2012). In particular, key research can be to date focused on issues of relevance for canyon ecology at the largest cabled observatory network on the planet, as operated by Ocean Network Canada (ONC; <http://www.oceannetworks.ca/>). The North East Pacific Time-Series Experiment, (NEPTUNE) network deployed in Barkley Canyon allows to study in situ rhythmic behavior and species tolerance in response to tidal and inertial fluxes (which has important implications on adult dispersal rates; Sbragaglia et al., 2015; Chatzievangelou et al., 2016), and to multiple climate change variables including methane, pH, pCO₂, pO₂, salinity, temperature, turbidity, chlorophyll-a (for primary production) (Purser et al., 2013). Such monitoring capability can be to date increased by endowing fixed networks of cabled monitoring platforms with semi-mobile rovers, tethered to the nodes, extending the spatial coverage from few m² to few tens of m² (Thomsen et al., 2012; Aguzzi et al., 2015). In the NW Mediterranean, the Operational Observatory of the Catalan Sea (OOCs; http://www2.ceab.csic.es/oceans/index_en.html) is a permanent pelagic buoy anchored at 200 m depth at the head of Blanes Canyon (Bahamon et al., 2011). This multiparametric pelagic platform, which also hosts a meteorological station, provides important data from the surface down to approximately 50 m depth on light intensity, chlorophyll, and productivity processes that influence the canyon trophic structure *via* atmosphere and water column (benthopelagic coupling mediated) interactions.

Addressing Knowledge Gaps for Human Impacts on Canyons

While it is becoming increasingly clear that human activities are impacting canyons, in order to set up effective mitigation strategies, the effects of different natural and anthropogenic impacts need to be better quantified. The studies that have reported on the impact of bottom trawling around La Fonera Canyon are excellent examples (e.g., Puig et al., 2012; Martín et al., 2014a,b; Pusceddu et al., 2014). But, similar work should be carried out around other canyons affected by bottom-trawling fisheries to obtain a more complete, and ideally global-scale, evaluation of the problem. In addition, the impact of other fishing techniques such as long-lining and fishing-related impacts such as ghost fishing, also need to be better quantified. Similarly, the impacts of litter, mine tailings, and chemical pollutants in canyons should be investigated on a wider scale. Should drilling for oil and gas in canyons become a reality, the potential impact of this activity will require particular consideration because of the

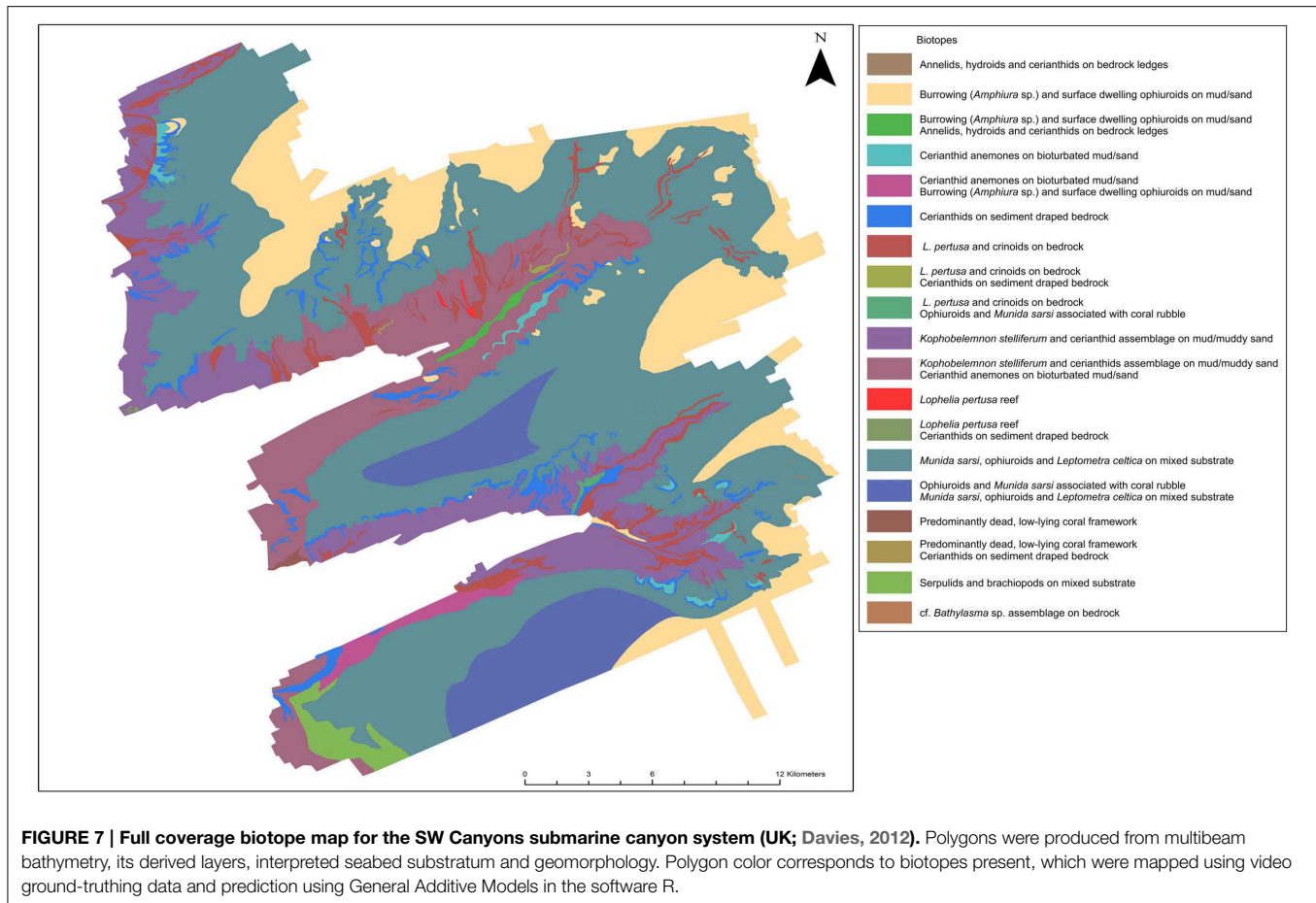
difference between canyon habitats and the typically more open locations of current deep-water drilling activities.

Given the level of human impact already observed within some canyon systems, it would be beneficial to understand both the resistance and resilience of canyon communities. Decisions on which human activities require management measures in order to mitigate adverse impacts rely on understanding the impacts (both acute and chronic) of those activities, and the potential for affected communities to recover. There are very few data available on community recoverability in canyons. With the designation of a number of previously impacted canyons as MPAs comes a unique opportunity to monitor the recovery (or otherwise) of these systems.

Finally, climate change-related impacts require investigation. Climate change will affect submarine canyons, for example, through increases in water temperatures, change in current patterns, and ocean acidification. Using a variety of modeling approaches, the impact of future climate scenarios needs to be evaluated in order to inform management strategies for canyons. Questions to address include; what will be the effect of changing water column density on internal wave and tide generation within submarine canyons? How will canyon species change their distribution patterns in a warming ocean? And how sensitive will canyon coral communities be under a shoaling aragonite saturation horizon? Given our current limited understanding of species distribution patterns, connectivity and vulnerability within submarine canyons, these questions are challenging. However, their outcome may have important implications for conservation strategies in the longer term.

Knowledge Gaps that Influence the Effective Implementation of Conservation Policy

To enable effective conservation and ultimately management of submarine canyons, it is necessary to develop tools that allow environmental managers to make informed choices and prioritize areas in need of protection. One approach to this is through the use of a top-down classification system, where divisions can be made on the basis of useful surrogates for biological diversity (Howell, 2010). For example, biogeographical region, water mass structure, seabed topography/geomorphology, depth, and substratum (Greene et al., 1999; Allee et al., 2001; Butler et al., 2001). **Figure 7** shows a complete biotope map for the SW Canyons submarine canyon system (UK), and illustrates the type of product needed by managers to make informed decisions about conservation efforts. The rationale for this approach is that different physical classes represent different biological assemblages, and thus enable an assessment of the criterion of representativeness of an MPA network (Evans et al., 2015), a major criterion of assessment of network effectiveness recommended by IUCN guidelines for highly protected areas (IUCN, 1994). This approach can only be effective if the major physical drivers of biological diversity within canyon systems are understood and adequately represented by available physical data sets. Understanding the relative importance of different drivers and measuring them,



is an area in which more research is needed—with a focus on comparing canyons with different physical environmental regimes in order to clarify the role of potential physical drivers in influencing differences in faunal communities and ecosystem function.

While top-down classifications can help design and facilitate broad-scale assessments of MPA networks, the degree to which these coarse classification systems represent finer-scale distribution of biological assemblages is still questionable (Williams et al., 2009). In addition, they do not allow the identification of areas where assemblages and species recognized as VMEs or in need of special protection measures are located. Habitat suitability modeling (also called species distribution modeling and predictive habitat mapping) offers a means to produce maps of the distribution of specific species and/or communities, within and between canyon systems. Its potential use in deep-sea conservation and management has been demonstrated in other deep-sea habitats (Piechaud et al., 2015) and across deep-sea regions (Ross and Howell, 2013). However, production of such maps again requires a robust biological classification system (where communities are considered) as well as a firm understanding of the drivers of community and species distributions. Progress in this area was made recently for canyons (Howell et al., 2010; Davies et al., 2014) but with limited spatial coverage. Further work is needed to improve

habitat suitability models for canyon species, expand their number, and to cover wider geographical areas. Constructing such models will also help to improve our understanding of the links between physical drivers and biological responses in canyons.

One of the key areas in which research is lacking is an understanding of connectivity both within and between canyons systems. Knowledge of population connectivity, constituting larval dispersal, settlement, survival and successful reproduction, is key for effective marine conservation (Gaines et al., 2003) and is called for many different policy documents. Our knowledge of gene flow within and between canyon systems is very limited, but recent data suggest there may be significant barriers to dispersal between canyons for some species (Pérez-Portela et al., 2016). If barriers to gene flow exist between canyons, then this must be considered when designing spatial management strategies.

CONCLUSIONS

With continuous demand for minerals, fish and genetic resources, international interest in submarine canyons is increasing. However, many knowledge gaps remain in many regions regarding abiotic and biological processes in canyons. These issues must be addressed in order to provide the robust

scientific knowledge necessary for effective management and conservation. This review demonstrates the need for further investigations to increase our understanding of community structure and ecosystem functioning within and around canyons. Future survey efforts need to incorporate rigorous and standardized sampling to obtain information regarding microhabitats, current flow, and organic matter input within the broad-scale habitat features. Such environmental data are required to better determine the mechanistic factors that affect the diversity, abundance, and distribution of fauna associated with these deep-sea habitats. There are new technologies and analytical methodologies that need to be used to efficiently and effectively provide the scientific understanding of canyons that is required.

Although we provide here the first global assessment of canyon protection, there is a need for this assessment to be augmented by an understanding of the level impacts that canyons face globally. Thus, there needs to be a compilation and synthesis of global information on impacts affecting canyons, the studies conducted to assess those impacts, and the protective and management measures taken to address these impacts. However, this information is currently sparse, non-structured and in some cases, available only in gray literature such as national or regional reports and, thus, difficult to access. This gap in global understanding of canyon impacts and management and conservation measures needs to be addressed by future studies, along with aforementioned ecological studies, if we are to achieve a global understanding of the role played by canyons in the functioning of the biosphere, the services they provide

and what measures are needed to exploit their resources in an environmentally-sustainable way.

AUTHOR CONTRIBUTIONS

UF coordinated, supervised, edited, and act as corresponding author. UF, ER, JA, ALA, JD, AD, PH, KH, VH, MM, JM, LM, MN, PP, AR, FS, and IV wrote the manuscript and helped in the revision and evaluation of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <http://journal.frontiersin.org/article/10.3389/fmars.2017.00005/full#supplementary-material>

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Annex I. Summarize the total number of canyons within a country/jurisdiction, the number (N) and percentage (%) with at least 10% of their area within MPAs and the number (N) and percentage (%) with 100% of their area within MPAs.

Country/Jurisdiction	No. Canyons	Canyons 10% in MPA		Canyons 100% in MPA	
		No.	%	No.	%
ABNJ	418	3	0.7	1	0.2
Alaska	430	193	44.9	136	31.6
Algeria	93	0	0.0	0	0.0
American Samoa	5	1	20.0	0	0.0
Andaman and Nicobar	63	0	0.0	0	0.0
Angola	21	0	0.0	0	0.0
Anguilla	19	1	5.3	0	0.0
Antarctica	550	12	2.2	10	1.8
Antigua and Barbuda	13	0	0.0	0	0.0
Argentina	30	0	0.0	0	0.0
Aruba	1	0	0.0	0	0.0
Australia	714	307	43.0	232	32.5
Australia - East Timor	1	0	0.0	0	0.0
Azores	33	0	0.0	0	0.0
Bahamas	43	0	0.0	0	0.0
Bangladesh	1	0	0.0	0	0.0
Barbados	12	1	8.3	0	0.0
Belize	13	4	30.8	2	15.4
Benin	2	0	0.0	0	0.0
Bonaire	2	0	0.0	0	0.0
Bouvet Island	7	0	0.0	0	0.0
Brazil	160	0	0.0	0	0.0
British Indian Ocean Territory	27	27	100.0	27	100.0
British Virgin Islands	15	0	0.0	0	0.0
Brunei	3	0	0.0	0	0.0
Bulgaria	10	0	0.0	0	0.0
Cameroon	1	0	0.0	0	0.0
Canada	145	2	1.4	0	0.0
Canary Islands	38	5	13.2	1	2.6
Cape Verde	19	0	0.0	0	0.0
Cayman Islands	30	0	0.0	0	0.0
Chile	182	0	0.0	0	0.0
Colombia	36	0	0.0	0	0.0
Colombia - Jamaica	2	0	0.0	0	0.0
Comoro Islands	9	0	0.0	0	0.0
Conflict Zone	8	0	0.0	0	0.0
Costa Rica	20	1	5.0	0	0.0
Croatia	1	0	0.0	0	0.0
Crozet Islands	11	2	18.2	0	0.0
Cuba	117	6	5.1	0	0.0
Curacao	4	0	0.0	0	0.0
Cyprus	21	0	0.0	0	0.0
Democratic Republic of the Congo	1	1	100.0	1	100.0
Djibouti	1	1	100.0	1	100.0
Dominica	7	3	42.9	0	0.0
Dominican Republic	70	18	25.7	16	22.9

East Timor	9	0	0.0	0	0.0
Easter Island	1	0	0.0	0	0.0
Ecuador	15	1	6.7	0	0.0
Egypt	32	0	0.0	0	0.0
El Salvador	9	0	0.0	0	0.0
Equatorial Guinea	2	0	0.0	0	0.0
Eritrea	1	0	0.0	0	0.0
Faeroe Islands	7	0	0.0	0	0.0
Falkland Islands	27	0	0.0	0	0.0
Fiji	96	0	0.0	0	0.0
France	84	52	61.9	42	50.0
French Guiana	8	0	0.0	0	0.0
French Polynesia	40	0	0.0	0	0.0
Gabon	9	0	0.0	0	0.0
Gambia	5	0	0.0	0	0.0
Georgia	10	1	10.0	0	0.0
Ghana	28	0	0.0	0	0.0
Gibraltar	1	1	100.0	0	0.0
Glorioso Islands	5	5	100.0	5	100.0
Greece	182	0	0.0	0	0.0
Greenland	106	0	0.0	0	0.0
Grenada	7	0	0.0	0	0.0
Guadeloupe	10	10	100.0	10	100.0
Guatemala	8	0	0.0	0	0.0
Guinea	12	0	0.0	0	0.0
Guinea Bissau	10	0	0.0	0	0.0
Guyana	2	0	0.0	0	0.0
Haiti	33	0	0.0	0	0.0
Hawaii	156	94	60.3	94	60.3
Heard and McDonald Islands	13	4	30.8	3	23.1
Honduras	38	4	10.5	0	0.0
Iceland	8	0	0.0	0	0.0
Ile Europa	3	3	100.0	3	100.0
India	71	0	0.0	0	0.0
Indonesia	576	20	3.5	4	0.7
Iran	10	0	0.0	0	0.0
Ireland	56	4	7.1	0	0.0
Israel	1	0	0.0	0	0.0
Italy	162	20	12.3	16	9.9
Ivory Coast	19	0	0.0	0	0.0
Jamaica	37	0	0.0	0	0.0
Jan Mayen	5	2	40.0	2	40.0
Japan	320	0	0.0	0	0.0
Japan - South Korea Conflict Zone	7	0	0.0	0	0.0
Juan de Nova Island	1	0	0.0	0	0.0
Kenya	18	0	0.0	0	0.0
Kenya/Somalia	1	0	0.0	0	0.0
Kerguelen Islands	17	0	0.0	0	0.0
Kiribati	35	0	0.0	0	0.0
Lebanon	5	0	0.0	0	0.0
Liberia	19	0	0.0	0	0.0
Libya	35	0	0.0	0	0.0
Line Group	5	0	0.0	0	0.0
Macquarie Island	65	27	41.5	20	30.8

Madagascar	84	0	0.0	0	0.0
Madeira	7	0	0.0	0	0.0
Malaysia	11	0	0.0	0	0.0
Maldives	21	0	0.0	0	0.0
Malta	15	0	0.0	0	0.0
Marshall Islands	38	0	0.0	0	0.0
Martinique	10	10	100.0	10	100.0
Mauritania	8	0	0.0	0	0.0
Mauritius	90	0	0.0	0	0.0
Mayotte	4	4	100.0	4	100.0
Mexico	174	2	1.1	1	0.6
Micronesia	22	0	0.0	0	0.0
Montserrat	1	1	100.0	1	100.0
Morocco	16	0	0.0	0	0.0
Mozambique	22	3	13.6	1	4.5
Myanmar	17	0	0.0	0	0.0
Namibia	29	0	0.0	0	0.0
New Caledonia	116	95	81.9	69	59.5
New Zealand	232	54	23.3	41	17.7
Nicaragua	27	0	0.0	0	0.0
Nigeria	15	0	0.0	0	0.0
Norfolk Island	47	45	95.7	40	85.1
North Korea	13	0	0.0	0	0.0
Northern Mariana Islands and Guam	89	12	13.5	10	11.2
Northern Saint-Martin	2	2	100.0	2	100.0
Norway	12	0	0.0	0	0.0
Oman	76	0	0.0	0	0.0
Pakistan	18	0	0.0	0	0.0
Palau	29	1	3.4	0	0.0
Panama	36	2	5.6	0	0.0
Papua New Guinea	265	1	0.4	0	0.0
Paracel Islands	12	0	0.0	0	0.0
Peru	38	0	0.0	0	0.0
Philippines	265	9	3.4	2	0.8
Portugal	36	0	0.0	0	0.0
Prince Edward Islands	5	5	100.0	5	100.0
Puerto Rico of the United States	49	3	6.1	1	2.0
Republique du Congo	1	0	0.0	0	0.0
Romania	3	0	0.0	0	0.0
Russia	219	3	1.4	0	0.0
Saba	2	0	0.0	0	0.0
Saint Kitts and Nevis	1	0	0.0	0	0.0
Saint Lucia	5	1	20.0	0	0.0
Saint Pierre and Miquelon	2	0	0.0	0	0.0
Saint Vincent and the Grenadines	6	0	0.0	0	0.0
Samoa	21	0	0.0	0	0.0
Sao Tome and Principe	3	0	0.0	0	0.0
Saudi Arabia	10	0	0.0	0	0.0
Senegal	13	0	0.0	0	0.0
Seychelles	116	0	0.0	0	0.0
Sierra Leone	19	0	0.0	0	0.0
Solomon Islands	135	0	0.0	0	0.0
Somalia	73	0	0.0	0	0.0
South Africa	52	0	0.0	0	0.0

South Georgia and the South					
Sandwich Islands	59	55	93.2	53	89.8
South Korea	10	0	0.0	0	0.0
Southern Kuriles	11	0	0.0	0	0.0
Spain	123	24	19.5	5	4.1
Spratly Islands	4	0	0.0	0	0.0
Sri Lanka	46	0	0.0	0	0.0
Sudan	6	0	0.0	0	0.0
Sudan/Egypt	5	0	0.0	0	0.0
Suriname	4	0	0.0	0	0.0
Svalbard	44	0	0.0	0	0.0
Syria	9	0	0.0	0	0.0
Taiwan	48	0	0.0	0	0.0
Tanzania	8	0	0.0	0	0.0
Thailand	2	0	0.0	0	0.0
Togo	1	0	0.0	0	0.0
Tonga	32	0	0.0	0	0.0
Trinidad and Tobago	1	0	0.0	0	0.0
Tristan da Cunha	3	1	33.3	0	0.0
Tunisia	6	0	0.0	0	0.0
Turkey	65	0	0.0	0	0.0
Turks and Caicos Islands	14	0	0.0	0	0.0
Tuvalu	19	0	0.0	0	0.0
Ukraine	7	0	0.0	0	0.0
United Arab Emirates	1	0	0.0	0	0.0
United Kingdom	3	0	0.0	0	0.0
United States	237	117	49.4	103	43.5
Uruguay	8	0	0.0	0	0.0
Vanuatu	92	0	0.0	0	0.0
Venezuela	46	1	2.2	0	0.0
Vietnam	23	0	0.0	0	0.0
Virgin Islands of the United States	14	0	0.0	0	0.0
Wake Island	4	4	100.0	4	100.0
Wallis and Futuna	7	0	0.0	0	0.0
Western Sahara	17	0	0.0	0	0.0
Western Sahara/Mauritania	1	0	0.0	0	0.0
Yemen	44	0	0.0	0	0.0
Total	9507	1291	13.6	978	10.3

Annex II

Davies, J.S., Guillaumont, B., Tempera, F., Vertino, A., Beuck, L., Ólafsdóttir, S.H., Smith, C., Fosså, J.H., **Van den Beld, I.M.J.**, Savini, A., Rengstorf, A., Bayle, C., Bourillet, J.-F., Arnaud-Haond, S., Grehan, A. (2017). A new classification scheme of European cold-water coral habitats: implications for ecosystem-based management of the deep sea. *Deep-Sea Research II*, *in press*.
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A new classification scheme of European cold-water coral habitats: Implications for ecosystem-based management of the deep sea

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A B S T R A C T

Cold-water corals (CWC) can form complex structures which provide refuge, nursery grounds and physical support for a diversity of other living organisms. However, irrespectively from such ecological significance, CWCs are still vulnerable to human pressures such as fishing, pollution, ocean acidification and global warming

Providing coherent and representative conservation of vulnerable marine ecosystems including CWCs is one of the aims of the Marine Protected Areas networks being implemented across European seas and oceans under the EC Habitats Directive, the Marine Strategy Framework Directive and the OSPAR Convention. In order to adequately represent ecosystem diversity, these initiatives require a standardised habitat classification that organises the variety of biological assemblages and provides consistent and functional criteria to map them across European Seas. One such classification system, EUNIS, enables a broad level classification of the deep sea based on abiotic and geomorphological features. More detailed lower biotope-related levels are currently under-developed, particularly with regards to deep-water habitats (> 200 m depth).

This paper proposes a hierarchical CWC biotope classification scheme that could be incorporated by existing classification schemes such as EUNIS. The scheme was developed within the EU FP7 project CoralFISH to capture the variability of CWC habitats identified using a wealth of seafloor imagery datasets from across the Northeast Atlantic and Mediterranean. Depending on the resolution of the imagery being interpreted, this hierarchical scheme allows data to be recorded from broad CWC biotope categories down to detailed taxonomy-based levels, thereby providing a flexible yet valuable information level for management. The CWC biotope classification scheme identifies 81 biotopes and highlights the limitations of the classification framework and guidance provided by EUNIS, the EC Habitats Directive, OSPAR and FAO; which largely underrepresent CWC habitats.

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1. Introduction

1.1. Cold-water coral habitats

Due to the high biodiversity associated with coral-dominated habitats and their ecological significance as physical support, refuge or nursery area for other living organisms; interest in cold-water corals (CWC) has grown significantly throughout the last two decades (e.g. Freiwald et al., 2004; Bryan and Metaxas 2007; Henry and Roberts, 2007; O'Hara et al., 2008; Roberts et al., 2009). Because of their vulnerability to fishing activity (Rogers, 1999; Fosså et al., 2002; Roberts, 2002; Grehan et al., 2005; Waller et al., 2007), a number of CWC habitats were earmarked for conservation. In 2004, 'Lophelia pertusa reefs', 'coral gardens', 'carbonate mounds' and 'sea-pen and burrowing megafauna communities' were considered as 'threatened or declining' under the Oslo-Paris Convention for the Protection of the Northeast Atlantic (OSPAR Agreement 2004-6). In 2007, cold-water coral reefs and several types of coral gardens came under the definition of the 'Reefs' habitat listed in Habitats Directive (92/43/EEC, 1992) Annex I and in 2009, CWCs habitats were listed as Vulnerable Marine Ecosystems (VMEs) by the United Nations General Assembly (UNGA Resolution 61/105; FAO, 2009).

Early works typically associated CWC concentrations with geomorphological elevations, entirely or partly created by azooxanthellate frame-building coral species, known as CWC reefs, banks and mounds according to their size, shape and composition (e.g. Freiwald et al., 2004; Roberts et al., 2009). However, they are also abundant in other habitats spread throughout NE Atlantic margin, at shelf breaks and on the upper continental slope (De Mol et al., 2002; Freiwald et al., 2004; Roberts et al., 2009), as well as in areas of pronounced topographic relief such as the slopes of banks, submarine canyons, and seamounts (Genin et al., 1986; Frederiksen et al., 1992; MacIsaac et al., 2001; Auster et al., 2005; Davies et al., 2014, 2015) frequently associated with hard substrate (Freiwald et al., 1999; Bryan and Metaxas 2007). Recent studies have shown the presence of cold-water coral habitats in Mediterranean deep-sea environments, occurring on the top and flanks of coral-formed or coral-topped relief (e.g. Vertino et al., 2010; Rosso et al., 2010; Savini and Corselli, 2010; Savini et al., 2014; Lo Iacono et al., 2014; Savini et al., 2016) as well as along escarpments and canyon walls (e.g. Freiwald et al., 2009; Sanfilippo et al., 2012; Gori et al., 2013; Taviani et al., 2011, 2015). In order to take an ecosystem-based approach to managing deep-sea environments and achieve an ecologically-coherent network across biogeographic regions, it is essential that we develop and structure our understanding of the variety and distribution of these important benthic habitats or biotopes. Biotopes represent distinct biological assemblages associated with certain environmental factors such as substratum and depth (Dahl, 1908).

Combining habitat maps originating from national and international programmes is necessary, but this can only be done harmoniously if standardised terminology exists. To date deep-sea maps produced by different projects / countries cannot be combined because of a lack of an agreed deep-sea classification system and recognised and agreed definitions of mapping units.

1.2. Habitat classification schemes as a mapping prerequisite

A premise to biotope mapping is having a systematic inventory and consistent descriptions of the biological assemblages to be used as mapping units. Habitat classification schemes are instrumental to these exercises as they organise the diversity of biological units to be mapped in a structured and systematic way, ensuring consistency, repeatability and comparability between maps from different regions.

1.2.1. The EUNIS classification

A range of marine habitat classification schemes which are applic-

able to the deep sea exist, and include (i) those that are top-down schemes with a predominantly geological basis (e.g. Greene et al., 1999) and (ii) those that are hierarchical, nested, and aim at ultimately resolving biotopes, such as the European Nature Information System (EUNIS).

EUNIS is a European hierarchical habitat classification scheme that was designed to facilitate and standardise data collection and description of terrestrial, freshwater and marine environments across Europe. Developing such standards in a balanced and comprehensive way throughout the diversity of environments is vital to allow continuity of data when producing habitat maps. Within the marine category (split from terrestrial environments at level 1), the deep seabed is discriminated at level 2 (A6) and subsequently divided into zones on the basis of substrate (level 3) and benthic assemblages (level 4). Topographically-based deep-sea habitat complexes such as seamounts and canyons are also included in level 3, their hierarchical positioning and coherence with the rest of the classes is debatable. EUNIS currently fails to provide as much detail for deep-water habitats (> 200 m) as it does for shallow-water habitats (Galparsoro et al., 2012; Tempera et al., 2013).

1.3. Deep-sea environments

The first effort to describe seabed assemblages for use in the mapping of the broad deep-sea areas off the European shores is traditionally attributed to Le Danois (1948), who worked on the basis of dredged samples in the Bay of Biscay. More recently, with the dissemination of *in situ* still and video imagery as a method of sampling the benthos, descriptions of deep-sea benthic assemblages have advanced more rapidly (e.g. Laubier and Monniot, 1985; Howell et al., 2010; Vertino et al., 2010; Tempera et al., 2013; Davies et al., 2014, 2015; De Leo et al., 2014). However, these efforts are still restricted to smaller areas within national waters and a comprehensive biogeographical coverage is lacking.

This paper contributes to refining existing classification schemes by hierarchically organising the diversity of CWC biotopes inventoried under the project CoralFISH using seafloor imagery from the Northeast Atlantic and Mediterranean.

2. Methods

2.1. CoralFISH project

The CoralFISH project ran between 2008 and 2013 by a consortium of 17 institutes and small/medium enterprises from 11 countries receiving co-funding from the 7th Framework Programme. Its objective was to assess the interaction between CWCs, fish and fisheries in order to develop monitoring and predictive modelling tools for ecosystem-based management in the deep waters of Europe and beyond.

In its scope, six target areas spread out over the Northeast Atlantic Ocean and the Mediterranean Sea were studied: Northern Norway/eastern Norwegian Sea, Iceland, Porcupine Seabight/Rockall Trough, Bay of Biscay, Azores and the Ionian sector of the Mediterranean Sea (Fig. 1).

2.2. Habitat classification scheme

2.2.1. Cold-water coral habitat identification

A CWC habitat was defined where a coherent suite of conspicuous epibenthic organisms including CWCs (as defined by Roberts et al., (2009)) extended throughout a minimum estimated area of 25 m² (as observed by underwater cameras). Generally, the individual habitats catalogued: (i) were repeatedly observed in multiple seafloor photos or along a video footage stretch representing an area ≥ 25 m² and (ii) showed similar dominant species compositions in different locations. Areas with a high along-track turnover rate in dominant species were interpreted as transitional habitats and avoided in establishing typical

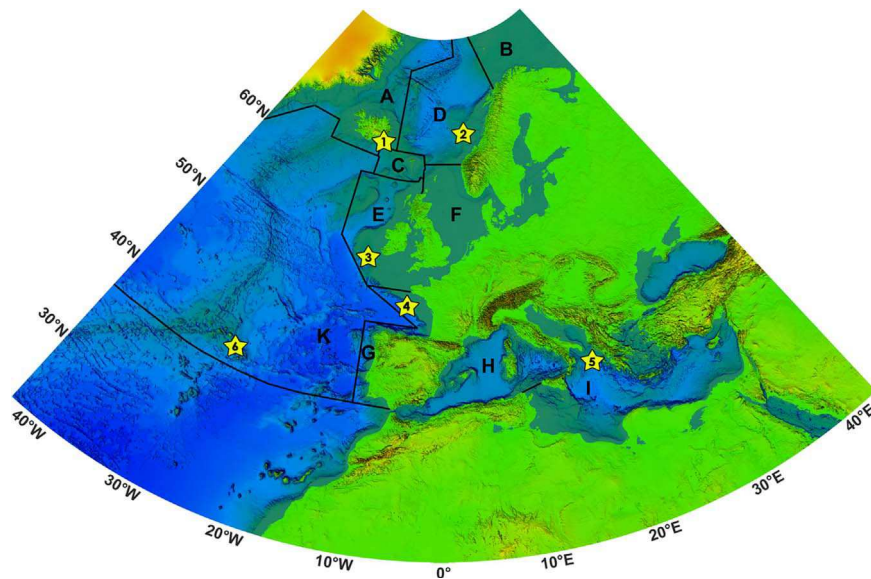


Fig. 1. Schematic representation of the six regional study areas of the CoralFISH project; their location is here referred to the corresponding European marine ecoregion, as defined from the Report of the ICES Advisory Committee on Fishery Management and Advisory Committee on the Ecosystem, 2004. The six study areas are located; (1) offshore south Iceland (ecoregion A); (2) offshore Norway (ecoregion D); (3) offshore western Ireland (Porcupine Bank and Seabight, and Rockall Trough; ecoregion E); (4) offshore western France (Bay of Biscay, ecoregion G); (5) offshore Italy and Greece in the Eastern Mediterranean sea (Northern Ionian sea, ecoregion I) and (6) in the Azores archipelago (ecoregion K).

species compositions.

The analyses spanned six major physiographic provinces between 200 and 3300 m depth, as explained below.

Imagery sources ranged from old discoloured slides from the late 1960s or aged VHS footage from the early 1990s to high-definition (full-HD) video and high-resolution digital photography from the early 2010s with resolutions as high as 3072×2304 pixels. Additional details can be found in Vertino et al. (2010), Savini et al. (2014), Rengstorf et al. (2014), Van den Beld et al. (in this issue), and Arnaud-Haond et al. (in this issue).

2.2.2. Geological classification

Following Harris et al. (2014) standardised geomorphological classification of the ocean seafloor were used for each level 3 biotope. Within the physiographic provinces investigated by the CoralFISH project, 6 major physiographic provinces were identified: 1. Continental shelf, 2. Continental slope, 3. Continental rise, 4. Oceanic islands and seamounts (including bathyal hills), 5. Large oceanic banks and plateaus (including slopes and summits), 6. Abyssal plains (on abyssal zone).

In all of the physiographic provinces investigated, CWC were associated with different geomorphic units. The terminology used to define geomorphic units was aimed at indicating (which recognises the importance of seafloor geomorphology in understanding the distribution of benthos) the main geomorphic features and substrate types which typify the locations in which CWC biotopes are known from the literature and/or characterised in the six CoralFISH study areas, as described below. Most of the terms used are also reported in standardised classification of ocean basins (although no official agreement exist between scientists in using the most appropriate terms for the different situations – MIM partnership, in press; Dove et al., 2016), for example the ones reported by the International Hydrographic Organisation (IHO, 2008) or by Harris et al. (2014) (Geomorphology of the oceans). Geomorphic units used in our work include *Carbonate mounds*, *Canyon systems*, *Mass-movement deposits* and *Submarine glacial landforms* that represent the major submarine landforms characterising the surveyed regions in the six CoralFISH study areas. In addition, *Bedrock and escarpments* were also considered to refer to those regions dominated by erosive processes or hard substrate or mixed sediments (including volcanic substrates forming volcanic cones or other volcanic

landforms); whereas those region of the bathyal plane that do not belong to common submarine landforms and are covered by soft sediment, were indicate as *Smooth and featureless slope regions*.

2.2.3. Habitat classification

The main factors taken into consideration in the habitat classification proposed were:

- (i) the dominant species or group of species.
- (ii) type of substrate, with the two main categories separating hard substrate (including mixed substrate and consolidated mud) and soft substrate; in particular cases, boulder habitats and vertical walls are also discriminated given the major changes in species and environmental conditions associated with them.
- (iii) the presence of coral framework (three-dimensional structure created by in-place scleractinians whose skeletons are in mutual contact and/or merged), with subordinate classes distinguishing alive or completely dead framework, the complexity of the 3D structure and the level of colonisation by other groups.

Some additional CWC habitats known from literature but not necessarily encountered in CoralFISH study areas were included with indication of sources, to provide a more comprehensive classification scheme.

The majority of the terminology used in Table 1 follows the CoralFISH glossary for underwater video analysis of European CWC habitats (Beuck et al., in prep).

2.2.4. Taxonomical identification

Emphasis was given to conspicuous habitat-building organisms and main characteristic species when establishing biotopes and the species composition list. Given the limitations in the resolution provided by many imagery sources, generally only taxa > 10 cm were identified. Where voucher specimens were not collected, the authors' taxonomic expertise and macroscopic correspondence to specimens in reference collections, or to referenced *in situ* taxa images, were used to establish the best taxonomic identification (i.e. high level of certainty to a given taxonomic level) of the organisms observed in the imagery. Despite the fact that non-calcified hydrozoans are not traditionally considered as corals, the habitats some of them form (e.g. order Leptothecata) share

Table 1

CoralFISH cold-water coral biotope classification scheme. The hierarchical scheme is set over three levels: biotope L1 incorporates dominant group of taxa and structure or the dominant group of taxa and substrate, biotope L2 incorporates dominant group of taxa, structure, density measures, substrate, and biotope L3 includes dominant subgroup of taxa, structures and/or substrate and/or secondary taxa groups and where relevant, geoform.

BIOTOPE - LEVEL 1 (dominant group of taxa, structure and/or substrate)	BIOTOPE - LEVEL 2 (dominant group of taxa, structure, density and/or substrate)	BIOTOPE - LEVEL 3 (dominant subgroup of taxa, structure and/or substrate and/or secondary taxa, geoform)	FINAL CODE
1. CW Scleractinian Reef	1. CW Scleractinian Reef	1. <i>Lophelia pertusa</i> Reef	1.1.1
		2. <i>Madrepora oculata</i> Reef	1.1.2
		3. Mixed <i>Madrepora oculata</i> and <i>Lophelia pertusa</i> Reef	1.1.3
		4. <i>Lophelia pertusa</i> and/or <i>Madrepora oculata</i> Reef with dense <i>Aphrocallistes</i> sp.	1.1.4
		5. <i>Lophelia pertusa</i> and/or <i>Madrepora oculata</i> Reef with dense free swimming Crinoids	1.1.5
	2. Colonised CW Scleractinian Reef	1. <i>Lophelia pertusa</i> Reef Colonised by <i>Primnoa</i> sp. and Plexauridae	1.2.1
		2. CW Scleractinian Reef Colonised by Antipatharians and/or Gorgonians	1.2.2
	3. Loosely-packed CW Scleractinian Framework with Soft Substrate	1. Loosely-packed <i>Lophelia pertusa</i> and/or <i>Madrepora oculata</i> Framework with Soft Substrate	1.3.1
	4. Colonised Loosely-packed CW Scleractinian Framework with Soft Substrate	1. Loosely-packed <i>Lophelia pertusa</i> Framework Colonised by <i>Primnoa</i> sp. and Plexauridae	1.4.1
		2. Loosely-packed <i>Lophelia pertusa</i> and/or <i>Madrepora oculata</i> Framework with Soft Substrate Colonised by Antipatharians	1.4.2
		3. Loosely-packed <i>Solenosmilia variabilis</i> Framework with Soft Substrate Colonised by Gorgonians	1.4.3
	5. Predominantly dead CW Scleractinian Reef	1. Isolated <i>Madrepora oculata</i> - <i>Lophelia pertusa</i> colonies on Framestones/Rudstones	1.5.1
		2. Isolated <i>Madrepora oculata</i> - <i>Lophelia pertusa</i> colonies on predominantly dead and low coral framework	1.5.2
	6. Dead CW Scleractinian Reef	1. Dead <i>Lophelia pertusa</i> and/or <i>Madrepora oculata</i> Framework with Brisingids	1.6.1
			2
2. CW Scleractinian Rubble	3. Colonial CW Scleractinians or Stylasterids on Hard Substrate	1. Dense <i>Lophelia pertusa</i> Framework on Vertical Wall	3.1.1
		2. Dense <i>Solenosmilia variabilis</i> Framework on Vertical Wall	3.1.2
		3. Dense <i>Eguchipsammia</i> Framework on Hard Substrate	3.1.3
	2. Colonised CW Scleractinian Framework on Hard Substrate	1. <i>Solenosmilia variabilis</i> Framework on Vertical Wall Colonised by Gorgonians	3.2.1
		2. <i>Solenosmilia variabilis</i> Framework on Vertical Wall Colonised by Ascidians	3.2.2
	3. Loosely-packed to Isolated colonies of CW Scleractinians on Hard Substrate	1. Isolated Colonies of <i>Lophelia pertusa</i> on Hard Substrate	3.3.1
		2. Isolated Colonies of <i>Madrepora oculata</i> on Hard Substrate (Vertical wall)	3.3.2
		3. Isolated Colonies of <i>Madrepora oculata</i> and <i>Lophelia pertusa</i> on Hard Substrate	3.3.3
		4. Isolated Colonies of <i>Madrepora oculata</i> and <i>Lophelia pertusa</i> on Hard Substrate with Euplectellidae	3.3.4
		5. Isolated Scleractinian Colonies on Boulders	3.3.5
	4. CW Stylasterids on Hard Substrate	6. <i>Dendrophyllia cornigera</i> on Hard Substrate/Mixed Substrate	3.3.6
		7. <i>Enallopsammia rostrata</i> on Hard Substrate	3.3.7
		1. <i>Errina dabneyi</i> and Sponges on Exposed Rocky Edges	3.4.1
	5. Dead CW Scleractinian Framework on Hard Substrate	2. <i>Cryptothelia</i> sp. on Hard Substrate	3.4.2
		1. Dead <i>Madrepora oculata</i> - <i>Lophelia pertusa</i> Framework on Hard Substrate	3.5.1
4. Solitary CW Scleractinians on Hard Substrate	1. Solitary CW Scleractinians on Hard/Mixed Substrate or Compact Mud	1. <i>Vaughanella</i> sp. on Hard Substrate Covered by Soft Substrate	4.1.1
		2. Solitary caryophyllids on Mixed Substrate	4.1.2
5. CW Alcyoniina on Hard substrate	1. CW Alcyoniina on Hard/Mixed Substrate or Compact Mud	1. <i>Anthomastus</i> sp. on Hard/Mixed Substrate or Compact Mud	5.1.1
		2. Nephtheidae on Hard/Mixed Substrate or Compact Mud	5.1.2
6. CW Antipatharians and/or Gorgonians on Hard Substrate	1. CW Antipatharians on Hard/Mixed Substrate or Compact Mud	1. Antipatharians on Hard Substrate	6.1.1
		2. <i>Antipathes dichotoma</i> on Hard Substrate with intense sedimentation	6.1.2
		3. <i>Leiopathes glaberrima</i> on Boulders	6.1.3
	2. CW Gorgonians on Hard/Mixed Substrate or Compact Mud	1. <i>Iridogorgia</i> sp. and other Gorgonians on Hard/Mixed Substrate	6.2.1
		2. <i>Chrysogorgia</i> sp. and <i>Acanella</i> sp. on Hard Substrate	6.2.2
		3. <i>Viminella flagellum</i> on Hard/Mixed Substrate	6.2.3
		4. <i>Viminella</i> sp. and <i>Dentomuricea</i> sp. on Hard/Mixed Substrate	6.2.4
		5. <i>Isidella elongata</i> on Hard/Mixed Substrate or Compact Mud	6.2.5
		6. <i>Narella</i> cf. <i>versluysi</i> on Hard Substrate	6.2.6

(continued on next page)

Table 1 (continued)

BIOTOPE - LEVEL 1 (dominant group of taxa, structure and/or substrate)	BIOTOPE - LEVEL 2 (dominant group of taxa, structure, density and/or substrate)	BIOTOPE - LEVEL 3 (dominant subgroup of taxa, structure and/or substrate and/or secondary taxa, geoform)	FINAL CODE
		7. <i>Primnoa resedaeformis</i> on Hard/Mixed Substrate or Compact Mud	6.2.7
		8. <i>Acanthogorgia</i> spp. and Large Primnoids on Hard/Mixed Substrate	6.2.8
		9. <i>Dentomuricea</i> sp. on Mixed Substrate	6.2.9
		10. <i>Swiftia pallida</i> on Hard/Mixed Substrate or Compact Mud	6.2.10
		11. Plexauridae spp. on Hard/Mixed Substrate	6.2.11
		12. <i>Paragorgia arborea</i> on Hard/Mixed Substrate	6.2.12
		13. Unidentified white coiled whip coral on Hard/Mixed Substrate	6.2.13
		14. cf. <i>Victorgorgia josephinae</i> on Hard/Mixed Substrate	6.2.14
7. Mixed CWC on Hard Substrate	7.1. Mixed CW Corals on Hard/Mixed Substrate or Compact Mud	1. Isolated colonies of Scleractinians, Antipatharians and Gorgonians on Hard/Mixed Substrate or Consolidated Mud	7.1.1.
		2. Isolated Colonies of Scleractinians, Antipatharians and Gorgonians on Hard Substrate Covered by Soft Substrate	7.1.2.
		3. <i>Primnoa</i> sp., Plexauridae and <i>Lophelia pertusa</i> on Hard Substrate	7.1.3.
		4. <i>Candidella imbricata</i> , <i>Lophelia pertusa</i> and various other Corals on Hard Substrate	7.1.4.
		5. <i>Paragorgia johnsoni</i> , <i>Anthomastus</i> sp. and Stylasterids on Hard Substrate	7.1.5.
		6. <i>Primnoa resedaeformis</i> and <i>Lophelia pertusa</i> on Vertical Wall	7.1.6.
		7. <i>Candidella imbricata</i> and <i>Leptopsammia</i> cf. <i>formosa</i> on Hard Substrate	7.1.7.
8. Mixed CWCs and Sponges on Hard substrate	8.1. Mixed CWCs and Sponges on Hard/Mixed Substrate or Compact Mud	1. <i>Lophelia pertusa</i> , Alcyoniina, Encrusting and Glass Sponges on Mixed Substrate	8.1.1.
		2. Large sponges and Isolated Scleractinian Colonies on Hard/Mixed Substrate or Compact Mud	8.1.2.
		3. Stylasterids, Primnoids, Alcyoniina and Large Sponges on Hard Substrate	8.1.3.
		4. Antipatharians, Short Sponges and Sparse Large Sponges on Hard Substrate	8.1.4.
		5. <i>Anthomastus</i> sp. with Lamellate Sponges and <i>Gorgonocephalus</i> on Hard Substrate	8.1.5.
		6. <i>Callogorgia verticillata</i> , <i>Asconema setubalense</i> and Demosponges on Hard Substrate	8.1.6.
9. Colonial Scleractinians on Soft Substrate	9.1. CW Colonial Scleractinians on Soft Substrate	1. Isolated Colonies of <i>Lophelia pertusa</i> and <i>Madrepora oculata</i> on Soft Substrate	9.1.1.
10. Solitary Scleractinians on Soft Substrate	10.1. CW Solitary Scleractinians on Soft Substrate	1. Solitary Caryophyllids and Xenophyophores on Soft Substrate	10.1.1.
		2. Flabellidae on Soft Substrate	10.1.2.
11. Gorgonians on Soft Substrate	11.1. CW Gorgonians on Soft Substrate	1. <i>Radicipes</i> sp. on Soft Substrate	11.1.1.
		2. <i>Callogorgia verticillata</i> on Soft Substrate	11.1.2.
		3. <i>Acanella</i> sp. on Soft Substrate	11.1.3.
		4. <i>Acanella arbuscula</i> and <i>Lepidisis</i> sp. on Soft Substrate	11.1.4.
		5. <i>Acanella arbuscula</i> and Unidentified Branched Coral on Soft Substrate	11.1.5.
12. Mixed CWCs on Soft Substrate	12.1. Mixed CWCs on Soft Substrate	1. <i>Thouarella</i> sp. and Seapens on Soft Substrate	12.1.1.
13. Mixed CWCs and Sponges on Soft Substrate	13.1. Mixed CW Corals and Sponges on Soft Substrate	1. <i>Acanella arbuscula</i> and <i>Hyalonema</i> spp. on Soft Substrate	13.1.1.
14. CW Seapens on Soft Substrate	14.1. CW Seapens on Soft Substrate	1. <i>Funiculina quadrangularis</i> and Burrowing Megafauna on Soft Substrate	14.1.1.
		2. cf. <i>Halipteris</i> sp. on Soft Substrate	14.1.2.
		3. <i>Kophobolemnion stelliferum</i> on Soft Substrate	14.1.3.
		4. <i>Pennatula</i> spp. on Soft Substrate	14.1.4.
		5. <i>Distichoptilum gracile</i> on Soft Substrate	14.1.5.
15. CW Hydrarians on Hard/Mixed Substrate	15.1. CW Hydrarians on Hard/Mixed Substrate	1. Hydrarians (cf. fam. Sertulariidae) on Hard Substrate	15.1.1.
16. CW Hydrarians on Soft Substrate	16.1. CW Hydrarians on Soft Substrate	1. <i>Lytocarpia myriophyllum</i> on Soft Substrate	16.1.1.

structural (and possibly functional) similarities with gorgonian gardens. They have thus been included in the definition of corals used in the CoralFISH glossary (Beuck et al., in prep) and the biotopes they structure integrate our classification scheme.

2.2.5. Correspondences with others classifications

Wherever possible, correspondence between our list of habitats and the following frameworks was put forward (i) Habitats Directive, (ii) OSPAR list of threatened and/or declining species and habitats, (iii) the EUNIS classification, and (iv) FAO/NEAFC Vulnerable Marine

Ecosystems (VMEs) (ICES Advice 2013, Book 1). As the FAO categories for VMEs are limited, the NEAFC proposed VMEs were used.

Coral gardens are defined in the scope of the OSPAR Convention as a relatively dense aggregation of colonies or individuals of one or more coral species. Following the CoralFISH glossary (Beuck et al., in prep), coral gardens can also be dominated by frame-building scleractinian species but differ from coral frameworks and reefs because coral skeletons are not in mutual contact and do not form large three-dimensional carbonate structures. Where no established criteria or statistical analyses were provided, assemblages were identified as

“potential coral garden”.

3. Results

The CWC habitats were classified into three biotope levels (Table 1): Biotope L1 is characterised by the dominant group of taxa and structure (e.g. reef, framework, rubble) or the dominant group of taxa and substrate typology (soft, mixed, hard); Biotope L2 is characterised by the dominant group of taxa, structure and density measure (e.g. dense or loosely-packed framework), substrate and presence of colonisation by other species and Biotope L3 is characterised by the dominant subgroup of taxa (defined at genus or species level where possible), structure and/or substrate and/or secondary group of taxa (colonisation) and, where relevant, geoform. Biotope level thereby relates to varying levels in taxonomic resolution, with level 1 being a low resolution category and 3 being a higher resolution category. Sixteen level 1 biotopes, 25 level 2 and 81 level 3 categories were identified (See Table 1). For some categories it was unclear if there was a placement for the corresponding categories under the listed habitats. In these instances, it was labelled as unclear (See Suppl Table 1).

The majority of these level 3 habitats correspond to habitats listed in directives and conventions: 66 fall under the OSPAR list of priority habitats, 62 under the Habitats directive and 71 fit the VME categories established by NEAFC. All 81 habitats could be classified using the substrate classification level in EUNIS, but only 9 corresponded to existing EUNIS biotopes (See Suppl (Guillaumont et al., 2016) for an illustrated CWC habitat catalogue and Suppl Table 1 for comparison with other habitat classification scheme and listed habitats). Note that the CMECS (Coastal and Marine Ecological Classification Standard) system developed by NOAA has been included in the Suppl Table 1 to allow comparison with the CoralFISH Scheme, and also to illustrate a more comprehensive scheme than the current European framework. As it is not a European-based system, it will not be discussed within this paper. For each biotope, associated metadata are given in the CWC catalogue (Suppl), with a list of the physiographic provinces and geomorphic units each biotope is associated with throughout the CoralFISH study area given in the Suppl Table 2.

4. Discussion

The large diversity of biotopes identified at different resolution levels demonstrates that not only imagery from recent expeditions but also historical photographic datasets represent valuable sources of information for deep-sea bionomy, even in situations where the original purpose of the surveys was not biotope recognition (e.g. geological exploration expeditions from the late 1960s up to the 1990s).

4.1. Listed habitats

The conservation-related habitat lists include only three habitats which relate to those biotopes described in the CoralFISH CWC scheme: cold-water coral reefs (OSPAR, Habitats Directive and VME), coral gardens (OSPAR, Habitats directive and VME), seapen communities (OSPAR and VMEs). These categories are widely used from an operational point of view (i.e. policy making) to give weight to habitats of conservation concern, and the CoralFISH CWC classification scheme presented here highlights a lack of taxonomic details that are of concern for the effectiveness of these categories. For example, under OSPAR, coral gardens are defined as ‘a habitat which has a relatively dense aggregation of individuals or colonies of one or more coral species which can occur on a wide range of soft and hard substrates’ (OSPAR 2010). In the context of hard substrate this habitat has been described as being dominated by gorgonian, stylasterid and/or antipatharian corals (ICES 2007) and can develop on exposed bedrock, boulders or cobbles (Roberts et al., 2009). The OSPAR definition of coral gardens is very broad, and the habitat in terms of biodiversity and densities of

associated species can vary with region, hydrography, topography, substrate and depth (OSPAR 2010), which is well demonstrated in our paper. To adequately protect such habitats, better criteria (including examples of coral garden habitats) are required to allow appropriate assessment and discrimination of the distinct habitat types embedded in this category (Bullimore et al., 2013).

The working definitions of listed habitats are restricted and vague. While some biotopes clearly adhere to those described under listed habitats, e.g. *Lophelia pertusa* reefs (1.1.1 in the proposed CoralFISH scheme) to ‘Biogenic reef’ (Annex I, Habitats Directive), ‘*Lophelia pertusa* reefs’ (OSPAR), and ‘deep-sea *L. pertusa* reefs’ (EUNIS); the placement of many others under these schemes is unclear. For example, when *Madrepora oculata* is the dominant reef-building coral none of the listed categories provides a good fit. Under the Habitats Directive only *L. pertusa* is mentioned, OSPAR only acknowledges the species as characteristic of the *Lophelia* dominated reefs and EUNIS can only be used if we take the unspecific level of ‘communities of deep-sea corals’.

4.2. Classification schemes

Existing habitat classification schemes are not adequate to support representative protection of vulnerable deep-sea biotopes such as those formed by cold-water corals. For example, under EUNIS, ‘Bioherms’ (large biological structures, formed by organisms such as corals or sponges) are not split up despite many authors reporting distinct assemblages associated with different bioherm zones [e.g. mostly live coral on coral mound summit; mostly dead framework and coral rubble on the flanks and surrounding seafloor; as described by Mortensen et al. (1995), Pfannkuche et al. (2004), Wienberg et al. (2008), Roberts et al. (2009), Vertino et al. (2010) and Davies et al. (2015)]. Additionally, in the EUNIS deep-sea bioherm section (A6.6) only one coral biotope is considered: Deep-sea *Lophelia pertusa* reefs. This does not reflect the range of deep-sea CWC bioherm biotopes identified by the CoralFISH inventory.

An objective, comprehensive and representative classification scheme using consistent terminology is required for describing the diversity of such habitats found across European seas. The CoralFISH CWC biotope classification scheme (i) addresses the shortcomings of other schemes, (ii) represents the regional variation of cold-water coral habitats and (iii) can be related to habitats listed in EU Directives and international Conventions.

The CoralFISH CWC classification scheme is compatible and could be included with CWC biotopes discrimination at EUNIS levels 4 to 6 - a proposal that is consistent with the perspective of the upcoming EUNIS revision (Doug Evans, unpublished data). It is assumed that at EUNIS level 3 deep-sea habitats are divided on the basis of substrate, which has been endorsed as a valid factor for deep-sea habitat classification (Howell, 2010).

In addition, unlike other classification schemes, the CoralFISH CWC classification subdivides scleractinian bioherms into live/dead reef, live/dead coral framework and rubble zones (*sensu* Mortensen et al. 1995) - an important feature given that these zones are known to vary in associated biodiversity (e.g. Jensen and Frederiksen, 1992; Mortensen et al., 1995; Freiwald et al., 2002, Rosso et al., 2010, Spezzaferri et al., 2013). The reef-building coral species are also distinguished, providing a better discrimination of these biotopes than OSPAR, which only accounts for *Lophelia pertusa* reefs and neglects other dominant species, for example the widely distributed *Madrepora oculata* (Arnaud-Haond et al., in this issue) that is a dominant framework-building species on some bathyal hills in the Azores or in the Mediterranean (Vertino et al., (2014) and reference therein). This is important from a conservation point of view and promotes the integration of improved representativeness into MPA networks.

4.3. Data resolution

Due to technical constraints and the high cost associated with deep-sea research, it is not feasible to collect full-coverage biological data (Diaz et al., 2004). For instance, approaches used for mapping shallow-water habitats based on satellite imagery are not applicable to the deep sea. Instead, the vast inaccessible area involved requires broad-scale sub-sampling and nested fine-scale surveys feeding into statistical models.

The methods used to acquire data determine the taxonomic resolution that may be achieved by subsequent analyses. The proposed hierarchical scheme allows data of varying resolutions to be represented. Given that resolutions of imagery datasets being interpreted vary greatly between equipment type, the CoralFISH scheme allows results to be recorded from broad cold-water coral categories down to finer detailed biotope level, thereby providing a flexible yet valuable information level for management.

The CWC habitat classification scheme provides much needed habitat descriptions which ought to be included into existing schemes such as EUNIS. At a nature conservation level, the results are instrumental to identify biotope occurrences that require protection under the Habitats Directive (reefs) and the OSPAR Convention (coral gardens, scleractinian reefs, seapens and burrowing megafauna communities, deep-sea sponge aggregations).

It should be noted that statistical methods (e.g. multivariate cluster analysis) were not employed to describe all level 3 biotopes. Undertaking a fully-quantitative analysis of deep-sea data is still very time-consuming due to the faunal complexity of many deep-sea habitats. Frequently it is also taxonomically-limited, as living specimens morphology is poorly documented for many species, which makes their visual identification difficult.

As the datasets explored during CoralFISH were broad and varied, such methods were not feasible for the entire dataset. Analytical methods may aggregate data at a resolution that is not ecologically significant, e.g. too small a unit, and therefore a non-statistical approach based on expert judgement may be necessary. Despite this, the hierarchical system which has been put into place still allows the inclusion of subsequently-defined biotopes when robust quantitative data and statistical analysis are available.

Finally, it must be emphasised that a detailed description of epibenthic assemblages requires further dedicated collections of voucher specimens and continued taxonomy research, preferably including molecular barcoding, on multiple animal groups which remain either unknown to science or visually irresolvable. In addition to a better identification of the organisms forming the biotope, further exploration of the deep-sea will potentially reveal biotopes not listed in the CoralFISH classification scheme, since the majority of the deep-seafloor still remains unexplored.

5. Conclusion

The analyses of a wide variety of imagery datasets from the Northeast Atlantic and Mediterranean within the project CoralFISH showed that the range of cold-water coral (CWC) biotopes is currently very poorly represented in the EUNIS classification system.

In order to address this, a new comprehensive hierarchical scheme is proposed incorporating this additional detail so that it can be readily embedded into the existing deep-sea EUNIS level 4–6. The proposed hierarchy is flexible in accommodating habitat data with different taxonomic resolutions, allowing occurrences from broad CWC biotope classes down to detailed taxonomy-based categories. This more detailed description and classification of CWC biotopes will facilitate the identification of biotope occurrences requiring protection under the Habitats Directive (reefs) and the OSPAR Convention (coral gardens, scleractinian reefs, seapens and burrowing megafauna communities). The proposed classification scheme will also permit more exact

associations of ecosystem functions, goods and services to marine habitats, setting the scene for assessments that are less prone to generalisations and provide more accurate maps at finer scales. (cf. MAES, 2014, Tempera et al., 2016).

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.dsr2.2017.04.014>.

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Annex III

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Two “pillars” of cold-water coral reefs along Atlantic European margins: Prevalent association of *Madrepora oculata* with *Lophelia pertusa*, from reef to colony scale

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ABSTRACT

The scleractinian coral *Lophelia pertusa* has been the focus of deep-sea research since the recognition of the vast extent of coral reefs in North Atlantic waters two decades ago, long after their existence was mentioned by fishermen. These reefs were shown to provide habitat, concentrate biomass and act as feeding or nursery grounds for many species, including those targeted by commercial fisheries. Thus, the attention given to this cold-water coral (CWC) species from researchers and the wider public has increased. Consequently, new research programs triggered research to determine the full extent of the corals geographic distribution and ecological dynamics of “*Lophelia* reefs”. The present study is based on a systematic standardised sampling design to analyze the distribution and coverage of CWC reefs along European margins from the Bay of Biscay to Iceland. Based on Remotely Operated Vehicle (ROV) image analysis, we report an almost systematic occurrence of *Madrepora oculata* in association with *L. pertusa* with similar abundances of both species within explored reefs, despite a tendency of increased abundance of *L. pertusa* compared to *M. oculata* toward higher latitudes. This systematic association occasionally reached the colony scale, with “twin” colonies of both species often observed growing next to each other when isolated structures were occurring off-reefs. Finally, several “false chimaera” were observed within reefs, confirming that colonial structures can be “coral bushes” formed by an accumulation of multiple colonies even at the inter-specific scale, with no need for self-recognition mechanisms. Thus, we underline the importance of the hitherto underexplored *M. oculata* in the Eastern Atlantic, re-establishing a more balanced view that both species and their yet unknown interactions are required to better elucidate the ecology, dynamics and fate of European CWC reefs in a changing environment.

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1. Introduction

According to Jones' definition (Jones et al., 1994), corals are considered as autogenic engineers as they “change the environment via their own physical structures, i.e. their living and dead tissues”. The population dynamics of these engineering species is determinant for

the dynamics of the communities they support and the persistence of ecosystems they belong to.

Two main species of stony corals form reefs in the East Atlantic (Fig. 1), the scleractinians *Lophelia pertusa* (Linnaeus 1758) and *Madrepora oculata* (Linnaeus 1758). Historical reports of locations of cold-water coral (CWC) reefs date back to the 18th century in Norway (Gunnerus 1768) and early 20th century in Ireland and the Bay of Biscay (Joubin, 1922a, 1922b; Le Danois, 1948) where massive formations were reported. In these reports, however, no distinction was made between *L. pertusa* and *M. oculata*, both referred to as “white corals”. These reef-building “white corals” were opposed to the

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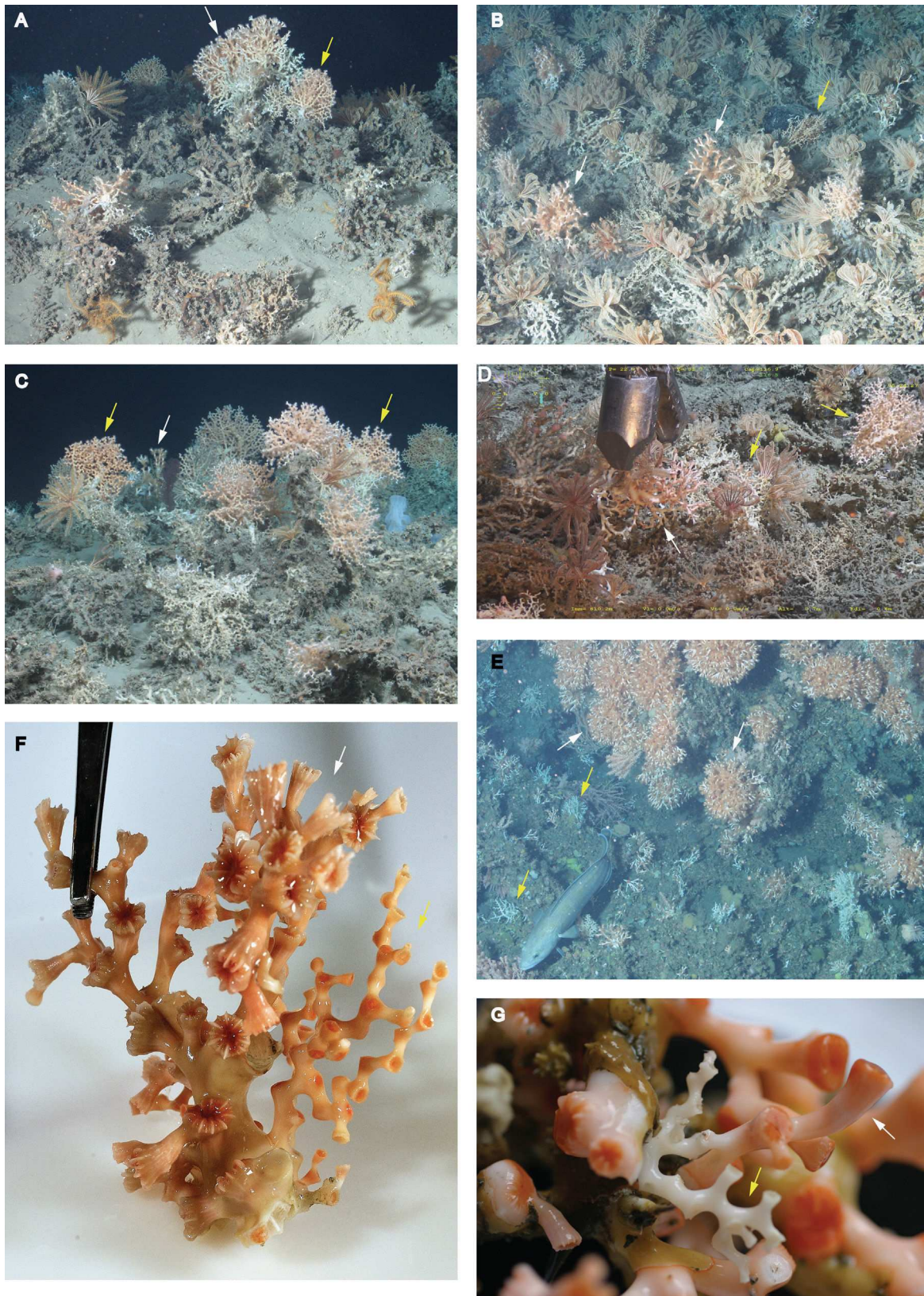


Fig. 1. Reefs showing the intermingling of both species (white arrow shows a *Lophelia pertusa* colony, yellow arrow a *Madrepora oculata* colony) in the Croisic (A), Guilvinec (B) and Petite Sole (C) canyons in the Bay of Biscay, at the Logachev Mounds region in Ireland (D) and at Hafadjúp off Iceland (E); (F, G) “chimaera”-like colony (white arrow shows a *Lophelia* polyp, yellow arrow a *Madrepora* polyp) sampled in the Bay of Biscay (F) and off Iceland (G).

“yellow” corals that included species from the genus *Dendrophyllia*, such as *Dendrophyllia cornigera* (Lamarck 1816). Fisheries moving to deeper areas and seabed surveys motivated by prospecting for fossil

energies (oil and gas) in the past two to three decades, have indeed led to the discovery of vast CWC reefs along continental margins (Rogers, 1999). The long-standing view that cold-water scleractinians would

most often occur as isolated colonies at high latitudes, with occasional occurrence of dense formations, was then challenged by the discovery of the large Sula reef dominated by *L. pertusa* on the mid-Norwegian shelf (Freiwald et al., 1999). Several reefs have been discovered and studied along European Atlantic margins in Norway and the Faroe Islands in the 90's (Frederiksen et al., 1992; Hovland et al., 1998; Hovland and Thomsen, 1997; Mortensen et al., 1995; Mortensen et al., 2001), followed by Ireland and the UK (Costello et al., 2005; De Mol et al., 2002; Roberts et al., 2003) and Sweden (Jonsson et al., 2004). Fosså et al. (2002) identified seven species of scleractinians occurring in Norwegian waters, of which only *L. pertusa* and *M. oculata* form reefs; these same authors also mentioned the lower abundance of *M. oculata* compared to *L. pertusa*, and that the former has never been reported to build reefs (Dons, 1944; Frederiksen et al., 1992). On a more recent quantitative study, Purser et al. (2013) also report a much lower abundance of *M. oculata* in the same waters. Possibly owing to the dominance of *L. pertusa* in the first explored reefs (Freiwald et al., 1999), this species remained the dominant focus of most subsequent cruises and ecological studies (Fig. 2) which target was often stated as “*Lophelia* reefs”, whereas *M. oculata* remained comparatively rather neglected up to the mid 2000's (Fig. 2).

More recent expeditions and historical record compilations (Reveillaud et al., 2008) have shed more light on the southern European margins, highlighting the frequent occurrence and engineering role of *M. oculata*, at least in the Bay of Biscay and in the Western and Central Mediterranean (Gori et al., 2013; Orejas et al., 2009; Vertino et al., 2010) that were less studied than Northern reefs. However, due to the relatively recent consideration of this species and to the logistic difficulties inherent to deep-sea sampling and observation, no quantitative estimates exist, thus far, to appraise the compared geographical distribution of *M. oculata* and *L. pertusa* in the Northeastern Atlantic. Species structuring habitat, referred to as “structural” (Huston, 1994), “ecosystem engineers” (Jones et al., 1994), or “founder” species (Bruno and Bertness, 2001; Dayton, 1975), have a major role as driver of the prospects of ecosystems and associated communities under environmental fluctuations (Peterson et al., 1984). Identifying these habitat-forming species and defining their potential and realised ecological niche (Bruno et al., 2003) to better understand their role as a driver of community composition and dynamics is a pre-requisite to most ecological studies including habitat modeling, the study of ecological interactions, the reconstruction of past history or the projection of future range shifts under environmental changes.

Here, we report on the observations made during two cruises taken place in 2011 and 2012, respectively, to locate reefs and appraise their extent in the Bay of Biscay, off Ireland and off south Iceland. We assessed the relative densities and seafloor area covered by both species in five sites sampled according to a

standardised scheme (Becheler et al., this issue) using random sampling of transects and video analysis. Results provide the first estimates of the relative abundances of the two scleractinian species found in reefs identified along Atlantic European margins, supporting an equivalent importance of *M. oculata* and *L. pertusa* in terms of abundance and spatial extent.

2. Material and methods

2.1. Study sites

During the BobEco cruise (September/October 2011), reefs from the Bay of Biscay and Celtic Sea were explored using the Remotely Operated Vehicle (ROV) Victor 6000 (Ifremer). The continental slope of the Bay of Biscay is regularly cut by a succession of submarine canyons connecting the continental shelf and the continental rise (Bourillet et al., 2003). In this area, CWC reefs formed by scleractinians were found to be typically located between 600 and 900 m depth, standing mostly above soft sediment. Five canyons were explored and sampled according to the procedure described in Becheler et al. (this issue), and standardised data were available for three of those canyons that are included in the present analysis (Le Croisic, Guilvinec and Petite-Sole; Fig. 3 and Table 1).

The Logachev Mounds region on Rockall Bank, off West-Ireland, North Atlantic Ocean, was sampled during the same cruise (Fig. 3 and Table 1). This area corresponds to multiple carbonate mounds colonised by CWCs, which are usually found at depths ranging from 500 to 1200 m (Mohn et al., 2014; van Haren et al., 2014). One dive was performed during the BobEco cruise in this area (Logachev, Fig. 3 and Table 1).

During the IceCTD cruise (June 2012), two reefs – Hafadjúp and Lonjúp – off South-Iceland in the North Atlantic, were also explored and sampled, of which one was analysed for this study (Hafadjúp, Fig. 3 and Table 1).

2.2. Sampling strategy

In order to optimise the likelihood of locating living reefs, the targeted locations were defined using geomorphological criteria, including depth, slope, the position compared to basin catchment, sediment structure (Bourillet et al., 2012a), and unpublished observations of the seafloor from imagery analysis of dives made during previous cruises. The dives consisted of (1) exploration of the area and (2) sampling for taxonomy, barcoding and population genetic purposes. Sampling strategy relied on the definition of sampling quadrats of a standard size (200 m* 100 m) in continuous areas of each reef. These quadrats have been used for assessing the density (expressed as colonies per m²) and coverage (expressed as m²) of the two main reef building corals (see below).

Within the quadrats, one to three colonies of both *L. pertusa* and *M. oculata* were sampled on each of 35 randomly drawn GPS positions (Becheler et al., this issue), resulting in a total of approx. 500 samples across eight locations including the five reefs analyzed in this study, of which the occurrence of “chimaera-like” (hetero-specific colonies) colonies was documented.

2.3. Density and coverage estimates through video analysis

During each sampling session, video frames from the quadrats were captured, and analyzed for an assessment of the density and coverage of *L. pertusa* and *M. oculata*. Using randomly generated times, 20 frame-grabs (N=20) were extracted from the downward-facing (vertically directed) camera (Fig. 4).

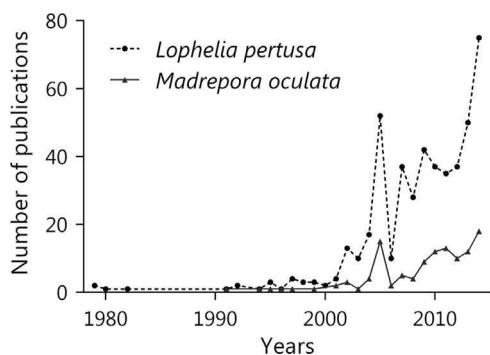


Fig. 2. Temporal evolution (cumulative) of the number of studies recorded in the Web of Science mentioning *Lophelia pertusa* (plain line) or *Madrepora oculata* (dot line) in the topic (including title, abstract and keywords).

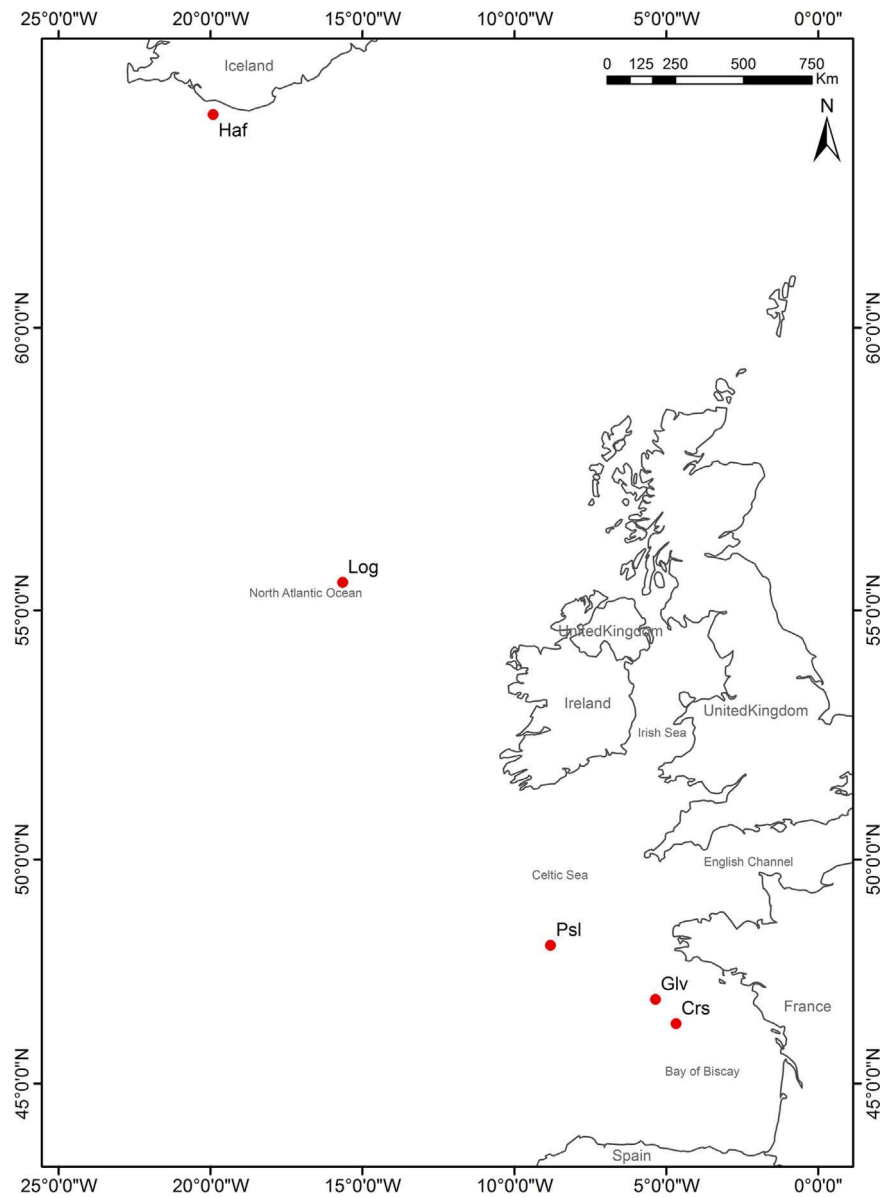


Fig. 3. Map of studied reefs (from South to North; Crs: Croisic, Glv: Guilvinec, Psl: Petite Sole, Log: Logachev Mounds, Haf: Hafadþúp). Projection is WGS 1984 World Mercator.

Table 1

Details of the regions and locations (with approximate depth) in which reefs were observed, including mean densities and the average surface areas covered (and standard deviation) of *M. oculata* and *L. pertusa*. Data correspond to 20 frame-grabs for each of 3 canyons in the Bay of Biscay, the Logachev Mounds region off Ireland and for Hafadþúp off Iceland. Significant differences in density and coverage documented for both species are indicated by bold values ($p < 0.05$).

Location (depth)	GPS coordinates	<i>Madrepora oculata</i>		<i>Lophelia pertusa</i>	
		Colony density (colonies per m ²)	Coral coverage (m ²)	Colony density (colonies per m ²)	Coral coverage (m ²)
Bay of Biscay					
Croisic (850 m)	46°23' 000 N4°41' 000 W	1.30 ± 1.42	0.02 ± 0.03	0.62 ± 0.76	0.01 ± 0.01
Guilvinec (850 m)	46°56' 043 N5°36' 0599 W	1.64 ± 1.19	0.04 ± 0.04	0.69 ± 0.90	0.02 ± 0.03
Petite Sole (650 m)	48°07' 320 N8°48' 800 W	0.53 ± 0.61	0.01 ± 0.02	0.02 ± 0.11	0.00 ± 0.00
Ireland (800 m)	55°31' 370 N15°38' 900 W	1.04 ± 0.80	0.02 ± 0.02	1.41 ± 1.61	0.03 ± 0.05
Iceland (400 m)	63°20' 430 N19°35' 800 W	0.12 ± 0.39	0.01 ± 0.03	0.26 ± 0.35	0.01 ± 0.02

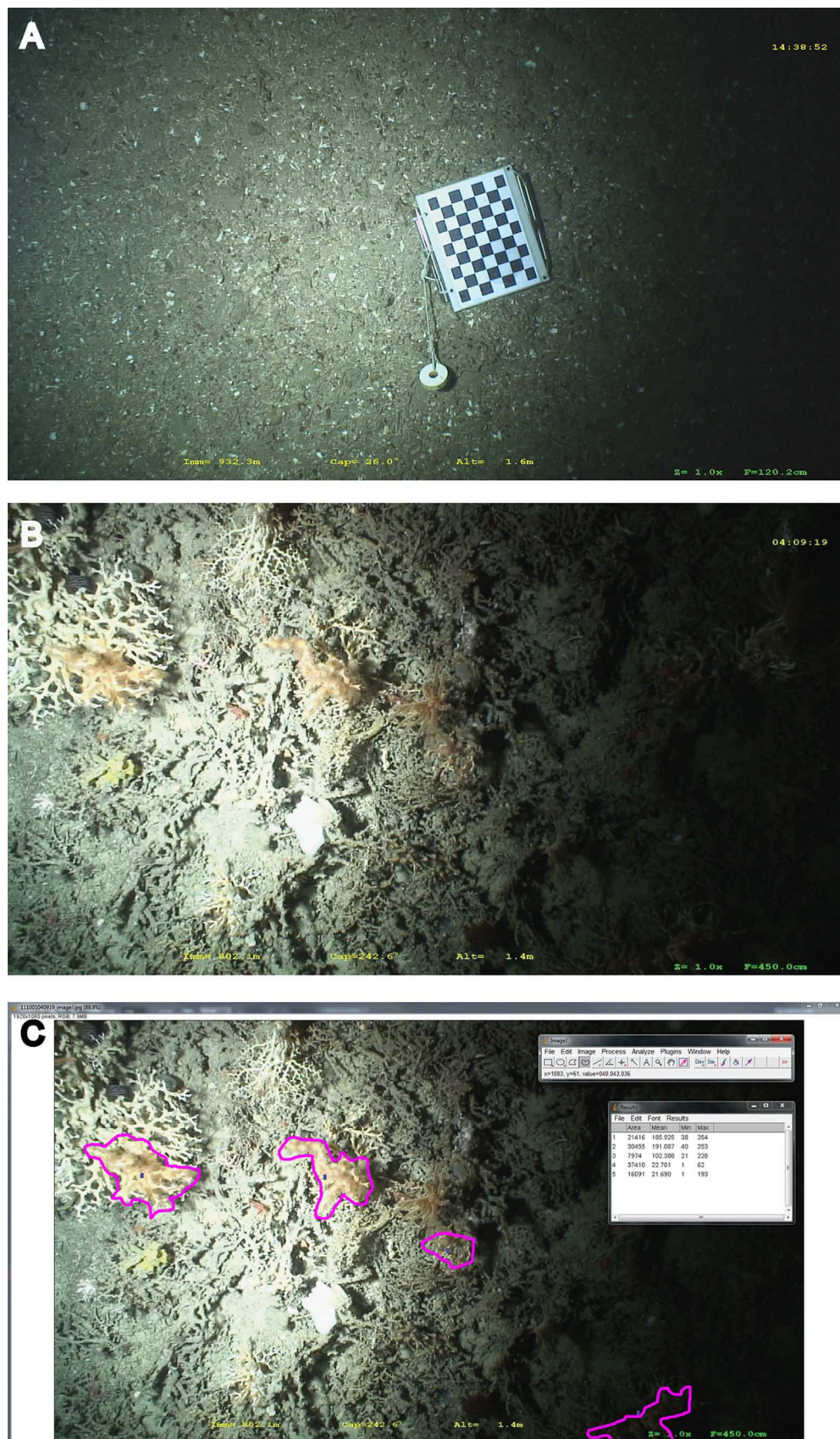


Fig. 4. An example of the method used to measure the coverage of the live colonies of *L. pertusa* and *M. oculata*. (A) The calibration grid used to calculate the total surface of a frame-grab, (B) an example of a frame-grab of the vertical camera of the ROV and (C) an example of a treated frame-grab from the Logachev Mounds region, Ireland, with ImageJ, including the contours of 4 live colonies.

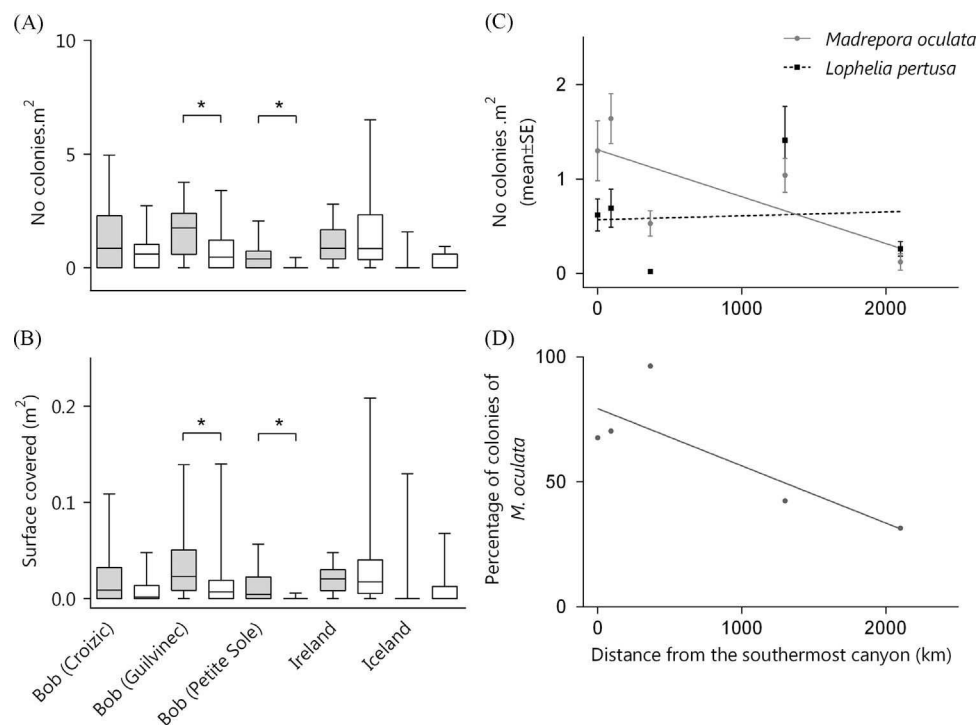


Fig. 5. Boxplots showing the (A) density of and (B) surface covered by *Madrepora oculata* (gray) and *Lophelia pertusa* (white) in standardized quadrats analyzed for 5 locations (Bob=Bay of Biscay), with significant differences indicated by stars, and the evolution of the relative (C) densities (no significant relationships, $R = 0.54$ $p = 0.15$ for *M. oculata*, $R = 0.00$ $p = 0.91$ for *L. pertusa*) and (D) proportions of both species when driving from southernmost canyon of Le Croisic in the Bay of Biscay to the northernmost reef of Hafadþúp off Iceland. No significant regressions were associated to the two last analysis ($R = 0.66$; $p = 0.09$).

Frame-grabs were excluded from analysis when they did not meet one or more of the following criteria: (i) the altitude of the ROV ranged between 0.8 m and 1.7 m, (ii) the quality of the frame-grab was higher enough to allow an unambiguous visual distinction between *L. pertusa* and *M. oculata* colonies, and (iii) the surface of the seabed was perpendicular (or nearly so) to the vertical camera's axis to avoid distortion of pictures. During sampling, the ROV was positioned on the seabed for several minutes, allowing the possibility that two or more frame-grabs may capture the same area of seabed. In these instances only one of the frame-grabs have been included in the analysis, thus ensuring that an area, and therefore the same colonies, would not be recorded more than once.

A grid was used to calibrate images from the vertical camera. The calibration grid was a pattern of black and white squares of 0.7 by 0.7 cm. The squares were measured on the image in pixel size and used as a scale to calculate the total surface of the seafloor visible on that image. In order to be conservative, calibration was done for a broad range of altitudes: between 0.5 and 5.0 m with 0.5 m intervals, measured by an altimeter on the ROV. The total surfaces of the frame-grabs at these sequential altitudes were used as a scale to estimate the area covered by each analysed image and provided a quantitative measurement of coverage, e.g. in m².

From each frame-grab the two scleractinian coral species *L. pertusa* and *M. oculata* were unambiguously identified using morphological criteria. Colonies were counted and the surface covered by them was measured to estimate (i) the density of live colonies of each species (colonies per square meter), (ii) the surface of live coral colonies (square meters covered by each species), (iii) the surface of dead coral framework and/or rubble (square meters covered by broken coral fragments), (iv) the surface of bare sediment, i.e. soft and/or hard substrate (square meters covered by the different substrate types) and (v) the surface of pebbles and cobbles (square meters covered by pebbles and cobbles). The free software program ImageJ (Schneider et al., 2012) was used to measure the seafloor surface occupied by the

live colonies, the dead rubble/framework, the bare sediment and the pebbles/cobbles. ImageJ allows the user to select areas and measure them in either pixel size or in a pre-defined unit if a scale has been set. The contours of each of the previous mentioned structures were selected by hand in ImageJ and the surface of these contours was calculated by the program in pixel size. In a later stage these surfaces in pixel sizes were converted to m² calibrated using the total surface of the image calculated using the previous mentioned grid. Comparisons of species density per m² were performed through a Mann-Whitney test within each sampling location, as the data were not normally distributed and variances were not homogeneous.

3. Results

During exploration dives (to find reefs), isolated colonies of the two reef-building scleractinians were observed outside of reefs during prospective dives in all three regions. These colonies were extremely frequent (pers. obs.) and were often made of a compound of both species growing next to each other or interspersed, resulting in "twin colonies".

Additionally, when samples were sorted on deck, four "chimaera-like" colonies formed of fully merged branches of *L. pertusa* and *M. oculata* were observed in the Bay of Biscay and in Iceland (Fig. 1F and G). Approximately 500 colonies were collected across 8 reefs including the 5 studied here, suggesting a prevalence of less than 1% of these "chimaera-like" colonies. The careful dissection of the junction zone between branches of both species of one of the colonies revealed the existence of a systematic calcareous wall containing soft tissues and preventing their admixture (Arnaud-Haond, pers. obs.), supporting these compound colonies as "false-chimaeras".

Regardless of latitude, all explored locations where reefs were recorded and investigated supported both *L. pertusa* and *M. oculata*

(Fig. 1A–E). The large patchiness in the distribution of colonies within reefs leads to relatively low averaged density but large variance. Their respective densities and coverage were similar within each location (Fig. 5A and B), with no significant departure detected (Mann–Whitney $p > 0.05$) except for two locations in the Bay of Biscay where *M. oculata* showed larger seafloor coverage and a higher density of colonies per m^2 than *L. pertusa* (Guilvinec, Coverage: $U=279$; $p=0.033$ Density: $U=298$; $p=0.007$; Petite Sole, Coverage: $U=322$; $p=0.001$ Density: $U=320$; $p=0.001$). For each species, the mean densities varied among locations, ranging from $0.02 \pm 0.11 \text{ col. m}^{-2}$ (colonies per square meter), which would imply a single colony per 50 m^2 , to $1.41 \pm 1.61 \text{ col. m}^{-2}$ for *L. pertusa* and from $0.12 \pm 0.39 \text{ col. m}^{-2}$ to $1.64 \pm 1.19 \text{ col. m}^{-2}$ for *M. oculata* (Table 1). In the Bay of Biscay, the mean seafloor coverage of *M. oculata* ranged between $0.010 \pm 0.01 \text{ m}^2$ (colony surface per explored square meter) and $0.038 \pm 0.04 \text{ m}^2$. The mean seafloor coverage of both Irish and Icelandic populations of *M. oculata* was in similar range, with mean coverage of $0.02 \pm 0.03 \text{ m}^2$ and $0.01 \pm 0.03 \text{ m}^2$ respectively (see Fig. 5B and Table 1). This parameter is less variable for *L. pertusa* with mean values ranging from very small (only $0.0003 \pm 0.001 \text{ m}^2$ in Petite-Sole) to $0.02 \pm 0.03 \text{ m}^2$ in the Bay of Biscay. The *L. pertusa* population of Logachev Mounds (Ireland) showed larger seafloor coverage with a mean area of $0.03 \pm 0.05 \text{ m}^2$, while the Icelandic colonies (Hafadjúp) showed slightly larger coverage than the minimum area range off France ($0.01 \pm 0.02 \text{ m}^2$; Fig. 5 and Table 1). An overall but not significant trend ($p=0.09$) toward a relative decline of *M. oculata* was observed from Southernmost to Northernmost locations (Fig. 5C and D), with similar non-significant trends retrieved in terms of seafloor coverage (data not shown).

4. Discussion

Here we propose a re-appraisal of the relative importance of both reef-forming scleractinians *M. oculata* and *L. pertusa* along Northeastern Atlantic European margins, based on most recent exploration cruises and on standardised strategy allowing a formal comparison of data among sites. Within Northeast Atlantic CWC reefs spanning from the Bay of Biscay to Iceland, our results revealed a quasi-systematic co-occurrence of *L. pertusa* and *M. oculata* at nested scales: the region, reef, and also often at the colony scale through the frequent observation of twin colonies. These results suggest the expression “*Lophelia* reefs” is not appropriate and possibly misleading at least for this part of the geographical range of distribution of the two coral species. The clear literature bias toward *L. pertusa* (Fig. 2), thus far, is likely due to the history of the discovery of CWC reefs in the North-East Atlantic, with most pioneer studies investigating corals off Norway (Dons, 1944; Frederiksen et al., 1992; Freiwald et al., 1999; Hovland et al., 1998; Hovland and Thomsen, 1997; Rogers, 1999). Our study is based on a standardised strategy and analyses of ROV images to allow a formal comparison of data among sites and therefore encloses only data from transects located in the zone from central Bay of Biscay to Iceland, without data available for Norway or Sweden, which makes the comparison with these well-studied areas presently impossible. Data presented here show that along the western European margins, *M. oculata* is at least as important or even more, in terms of colony density and spatial coverage, than *L. pertusa*, with a trend toward decreasing occurrence in the northern-most location of this study off Iceland. These results, together with the dominance of *L. pertusa* along the Norwegian shelves (Fossa et al., 2002; Mortensen et al., 1995; Purser et al., 2013; Roberts et al., 2009; Rogers, 1999), and the dominance of *M. oculata* in the Mediterranean (Freiwald et al., 2009; Gori et al., 2013; Orejas et al., 2009; Taviani et al., 2005; Vertino et al., 2010) suggest an inverse South–North shift in the relative abundance of

both reef-forming scleractinians (Fig. 5). Within the North-East Atlantic, this coexistence in comparable densities may indicate an overlapping of the ecological niches of both species. The data in Iceland are above all subjected to a large variance due to the high spatial heterogeneity in the distribution of large colonies forming Icelandic reefs, further data would, thus, be needed to formally test for the hypothesis of a general decline in *M. oculata* toward higher latitudes rather than just on Norwegian margins.

Whether this observation is reflecting a causal relationship with latitude induced, for example, by different changes of the environmental conditions due to rapid climate changes (Frank et al., 2011), or an influence of the peculiar seascape associated to CWC reefs encountered in the Bay of Biscay (sharp bathymetry and slopes in the canyons) cannot be disentangled. Recent studies showed clear physiological differences (growth rates, feeding ecology, metabolism, sensitivity to temperature and pH) between the two species (Gori et al., 2014; Hennige et al., 2014b; Lartaud et al., 2013; Maier et al., 2012; Movilla et al., 2014; Naumann et al., 2014; Orejas et al., 2011). While most of these works were based on Mediterranean specimens, some of these results may indicate that *L. pertusa* is better adapted to lower temperatures, while *M. oculata* seems to exhibit a greater ability to grow in warmer waters (Naumann et al., 2014). Notably, the current temperature of the Mediterranean Sea is likely the maximum viable one for *L. pertusa* as referred by Freiwald et al. (2009). Laboratory experiments on Mediterranean specimens of the two coral species have also demonstrated a more efficient thermal acclimation to lower temperatures for *L. pertusa* than *M. oculata* within their natural thermal range (Naumann et al., 2014).

Yet, most reefs identified and mapped during the BobEco cruise, as the ones reported here (Fig. 3) were located in areas characterized by specific geomorphological conditions including rather steep slopes ($10\text{--}40^\circ$), associated with the canyon flanks (Bourillet et al., 2012b). As a matter of fact, when explored areas (during BobEco, or the previous BobGeo and Evhoe cruises) exhibited flat or almost flat seascapes, some in the close vicinity of approximate locations initially reported by Joubin (1922a) and Le Danois (1948) as supporting extensive density of corals damaging trawling nets, no scleractinian masses were observed. At best isolated colonies could be recorded, that were often “twin” colonies of both species growing in the next to each other off-reef (Arnaud-Haond, pers. Obs.). In the Mediterranean, where CWC are mostly observed on cliffs in canyons, mounds and escarpments, *M. oculata* is largely dominant (up to 50 times more abundant in Cap de Creus or Lacaze-Duthiers canyons, Gulf of Lion) over *L. pertusa* (Gori et al., 2013; Orejas et al., 2009). *M. oculata* formations (being the species dominant over *L. pertusa*) have also been found in the Santa Maria di Leuca province (and other locations in the Ionian Sea), that show a rough seafloor topography, including ridges and scarps (Vertino et al., 2010). Contrastingly, in Ireland and Iceland much flatter areas characterized the locations where reefs were observed and studied. The relative importance (maximal densities) and patchiness (degree of aggregation) of *M. oculata* in our study may, thus, either be influenced by latitudinal gradients, or by some local differences in seascape such as slope steepness and availability of hard substrate (Orejas et al., 2009) or hydrodynamic currents controlled by the local bathymetry (Khripounoff et al., 2014). Additionally, life history differences between both species may lead to hypothesize a more “r” strategy for *M. oculata*, with a larval dispersal and settlement requirement promoting rapid colonization of newly available grounds and higher prevalence in less stable areas. Further data would be needed to explore those alternative drivers of the admixture of structural species forming CWC reefs in the North-East Atlantic. Nevertheless, paleogeographical records of CWC reefs in Mediterranean (Taviani et al., 2005) and Gulf of Cadiz (Wienberg et al., 2009) clearly suggest that *M. oculata* better tolerates environmental fluctuations than *L. pertusa* and the progressive warming of the Mediterranean after the end of the

Last Glacial Maximum (LGM, 11000 y.BP) affected the relative abundances of both species toward a dominance of *M. oculata*. For the Bay of Biscay, important changes in sea water temperature and sediment supply occurred just at the end of the LGM (between ca. 20 and 17 ka). A large discharge of meltwater due to the decay of the British and Fennoscandian ice-sheets arrived on the shelf and slope from the Fleuve Manche paleoriver (Toucanne et al., 2012; Toucanne et al., 2010), and a subsequent sediment discharge was delivered to the slope into the canyons between 17 and 8 ka (Toucanne et al., 2012). These facts, together with the recent results from eco-physiological studies (Gori et al., 2014; Hennige et al., 2014b; Lartaud et al., 2013; Maier et al., 2012; Movilla et al., 2014; Naumann et al., 2014; Orejas et al., 2011) and present data, indicate that the temperature range may, thus, be an important factor discriminating the distribution range and potential niches of both species that would, therefore, partially overlap. Additionally, *M. oculata*, appears more dominant in apparently heavily impacted areas where smaller reefs were observed in terms of height, and where most fishing gears and trawling marks were detected (Croisic and Guilvinec in particular; Van den Beld et al., this issue). This might be related due to different life-history traits of *M. oculata* compared to *L. pertusa*, including a faster growth (Orejas et al., 2011), or a possible quicker settlement after perturbations (differences in gametogenesis for example, or size of oocytes or larvae, ...), and may deserve further attention.

Colonies can be defined as structures attached to the substratum at one point (Stoddart and Johannes, 1978) and growing vertically by asexual reproduction of individual polyps, thus forming “ramets” (Harper, 1977; Hughes, 1989) such as all colonies grown from one larvae issued from a single event of sexual reproduction are belonging to the same clonal lineage (also called “genet”). The “false chimaeras” formed by a *M. oculata* and *L. pertusa* colony, one settled on the other, demonstrate the admixed nature of these structures that may better be considered as “coral bushes” (Wilson, 1979) composed of different genets settled on each other and intermingling through time (Fig. 1F and G). These observations thus reveal the common juxtaposition of multiple genets, due to the settlement of larvae on an implanted colony, rather than real chimaeras or hybrid colonies. First, in the absence of fusion of soft tissue or evidence of coenosarc structure bridging heterospecific polyps, this observations shows that self-recognition that was recently suggested in the case of “chimaera-like” colonies of *L. pertusa* (Hennige et al., 2014a) is not required to explain these formations. This may rather suggest that the calcareous skeleton of scleractinian corals can be considered as a substrate type that could facilitate settling and development of particles. However, observations made in the Bay of Biscay, Ireland (Logatchev mounds) and Iceland (Hafadjúp) also point toward an almost systematic occurrence of both species in the explored locations, including areas where only isolated bushes were recorded often exhibiting an admixture of both species either ‘merged’ (Fig. 1F and G) or settled next to each other (Fig. 1A–E). This suggests not only a strong overlap of their realised niche in the Bay of Biscay and Logatchev mounds, and to a lower extent in Hafadjúp, but also a possible positive interaction between species, i.e. the presence of one potentially facilitating the other (Bruno and Bertness, 2001; Bruno et al., 2003) that may be explored both experimentally and through habitat modeling in the Bay of Biscay. This colony juxtaposition brings back the term from Pêres and Piccard (1964) to the present times that was used to describe these coral communities in the Mediterranean, where they reported no named species dominance, i.e. “le biocenose des coraux blancs” (“biocenosis of white coral”), which following given our observations may be very appropriate.

As paleontological records show different responses to past climatic oscillations for both species, their distribution in the northeastern Atlantic may therefore evolve differently under

future environmental changes depending on their interaction in their potential and realised niches (Bruno et al., 2003; McGill et al., 2006). As a result, the comprehensive reconstitution of the influence of past climate changes on the biogeographic history of CWC reefs based on geochronological and genetic studies has to encompass both species. However, whereas isotopic studies performed thus far often included *M. oculata* (Frank et al., 2004; Frank et al., 2009; McCulloch et al., 2010; Montero-Serrano et al., 2013), no genetic studies thus far have concomitantly tackled the present day or past connectivity of *M. oculata* with that of *L. pertusa*. Similarly, there is a need to enhance knowledge of habitat suitability and sensitivity to environmental changes (Rengstorf et al., 2013) of *M. oculata*, as the occurrence of species communities supported by CWC reefs nowadays may depend on the persistence of both in part of their distribution ranges, or only one of the two habitat forming species.

5. Conclusion

In conclusion, CWC reefs along European margins are reliant on two pillars of scleractinian species, namely *L. pertusa* and *M. oculata*, as opposed to the current held misconceived view that only the former species provides vast structural habitats for a diverse community of associated species. The prevalence of *M. oculata* being more important than considered to date, particularly at lower latitudes, indicates that the designation of “Lophelia reefs” may thus not be adapted to most reefs along eastern Atlantic margins. These results suggest a complete overlap of realised niches in the Bay of Biscay with a possible divergence biased toward *M. oculata* in the Mediterranean and *L. pertusa* at higher latitudes, or at least in northeastern locations; resulting in an inverse gradient of density for both species with an increase of *M. oculata* and a decrease of *L. pertusa* from North to South. Altogether with a quasi-systematic occurrence of both species in the canyons of the Bay of Biscay, these observations call for further research to understand both the width and overlap of potential and realised niches for both species, and the way their interaction may lead to possible facilitation in some geographic areas. Finally, the observations of “false chimaera” from the Bay of Biscay to Iceland, despite a rather low sampling density, reveals the ability of larvae to settle on already established colony, an event that may occur as often or more among conspecifics without necessarily requiring self-recognition of colonies. The latter observation provides evidence that intra- (and inter-) specific diversity can be expected at the scale of what could, thus, be described as “coral bushes” formed by multiple homo- or heterospecific colonies growing interspersed.

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"Habitats coralliens dans les canyons sous-marins du Golfe de Gascogne: distribution, écologie et vulnérabilité"

Résumé

Les habitats de coraux d'eau froide formés par des scléractiniaires coloniaux, des gorgones, des antipathaires et des pennatules sont des hotspots de biodiversité et de biomasse. Ils fournissent des fonctions importantes, comme des refuges et des zones d'alimentation, pour d'autres organismes. Mais, ils sont également vulnérables aux activités humaines, parce qu'ils sont fragiles, croissent lentement et atteignent des records de longévité. Dans les canyons sous-marins, le relief tourmenté, l'hydrodynamisme et l'hétérogénéité des substrats offrent des conditions environnementales propices au développement des habitats coralliens. Dans le Golfe de Gascogne, les coraux d'eau froide sont connus depuis la fin de 19e siècle, mais leur distribution, leur densité et leur rôle fonctionnel avaient été très peu étudié.

Pour augmenter cette connaissance, 24 canyons sous-marins et 3 sites sur l'interfluve/haut de pente contigu aux canyons adjacents ont été visités par un ROV et une caméra tractée pendant 46 plongées au cours de 7 campagnes océanographiques. Les habitats coralliens définis par le système de classification CoralFISH ont été cartographiés à partir des images prises par les engins sous-marins puis la faune associée, les types de substrat et les déchets ont été annotés.

Onze habitats coralliens et 62 morphotypes de coraux ont été observés dans les canyons sous-marins du Golfe de Gascogne hébergeant 191 morphotypes de faune associée, dont 160 morphotypes uniques. Les patrons de distribution à l'échelle locale et à l'échelle régionale pourraient être liés aux régimes hydrodynamiques et sédimentaires. Le type de substrat était important pour les assemblages de coraux et leurs faunes associées, distinguant les habitats biogéniques, sur substrat dur et sur substrat meuble. Les assemblages de coraux étaient similaires entre habitats biogéniques et habitats sur substrat dur, mais la faune associée était plus abondante et diversifiée sur les habitats biogéniques. La diversité-alpha, -beta et -gamma étaient étonnement élevée sur les habitats coralliens sur substrat meuble, égalant ou dépassant la diversité des habitats biogéniques.

Les déchets marins étaient abondants et principalement composés de plastiques et de matériels de pêche. Ces déchets pourraient impacter les habitats coralliens : ils ont été trouvés à des profondeurs similaires et les déchets étaient piégés par des reliefs créés par des structures biologiques et géologiques. L'occurrence des récifs de coraux préférentiellement sur les pentes plus abruptes des canyons sous-marins tandis que les débris de coraux sont plus fréquents sur des aires plus plates de l'interfluve ou du haut de pente, pourraient indiquer un impact de la pêche.

Cette étude a contribué à l'initiative en cours de création d'un réseau Natura 2000 qui protégera à terme l'habitat 'récif' dont les habitats coralliens biogéniques et sur substrat dur, mais pas les habitats coralliens sur substrat meuble. Pour ces derniers, un complément d'étude et d'autres stratégies de préservation seront nécessaires.

Mots clés : coraux d'eau froide, récif de *Lophelia* et *Madrepora*, jardins de coraux, habitats coralliens, diversité, communauté de mégafaune associée, déchets marins, canyons sous-marins, Golfe de Gascogne, impact anthropique, vulnérable.

"Coral habitats in submarine canyons in the Bay of Biscay: Distribution, ecology and vulnerability".

Abstract

Cold-water coral (CWC) habitats formed by colonial scleractinians, gorgonians, antipatharians and sea pens are biodiversity and biomass hotspots that provide important functions, such as shelter and feeding grounds, to other organisms. But, they are also vulnerable to human activities, because they are long-lived, grow slowly and have a low resistance. Submarine canyons may offer the environmental conditions needed for CWC habitat development, due to their steep topography, complex hydrodynamics and substrate heterogeneity. In the Bay of Biscay, which margin is incised by hundreds of canyons, CWCs are known to exist since the late 19th century, but their distribution, density and functional role remained largely unknown, which impaired their preservation.

To increase this knowledge, 24 canyons and three locations between adjacent canyons were visited with an ROV and a towed camera system during 46 dives on 7 cruises. Images were analysed for CWC habitats using the CoralFISH classification system. Within these habitats, corals, associated fauna were identified and substrate cover measured. Litter was identified in 15 out of 24 canyons.

Eleven coral habitats constructed by 62 coral morphotypes were observed in the canyons of the Bay of Biscay hosting 191 associated megafaunal morphotypes, including 160 unique morphotypes. The distribution patterns at regional and local scales could be linked to hydrodynamics and sedimentary regimes. Substrate type was an important driver for coral and associated faunal assemblages, distinguishing biogenic, hard substrate and soft substrate habitats. Coral assemblages were similar between biogenic and hard substrate habitats, but the associated fauna was more abundant and diverse on biogenic habitats. The alpha, beta and gamma diversity was surprisingly high on soft substrate habitats, equalling or exceeding that of biogenic habitats.

Marine litter was abundant and was mainly composed of plastic items and fishing gear. Litter could co-occur with CWCs and impact them: litter and most CWC habitats were observed at similar water depths and litter was more abundant in areas with a seafloor relief created by biological or geological features. Observations of coral reefs on steeper areas in the canyons and coral debris on flatter areas on the interfluvial/upper slope may indicate a potential impact of the fishing industry.

This study supports the ongoing effort to create a Natura 2000 network that will protect biogenic and hard substrate habitats, but also points out the need to develop a framework for the preservation of coral habitats on soft substrate.

Keywords : cold-water corals, *Lophelia* and *Madrepora* reefs, coral gardens, coral habitats, diversity, associated megafaunal community, marine litter, submarine canyons, Bay of Biscay, anthropogenic impact, vulnerable.