

UNIVERSIDADE DOS AÇORES
DEPARTAMENTO DE OCEANOGRAFIA E PESCAS

**COLD-WATER CORAL COMMUNITIES
IN THE AZORES: DIVERSITY, HABITAT
AND CONSERVATION**



Dissertação submetida para obtenção do grau de Doutor no ramo Ciências do Mar,
especialidade em Ecologia Marinha

por
Andreia Filipa Domingues Braga Henriques

Horta, 2014

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Supervisor: Ricardo Serrão Santos PhD

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Joint publications produced as Ph.D. candidate relevant to this thesis

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8. Sampaio, Í., Braga-Henriques, A., Pham, C., Ocaña, O., de Matos, V., Morato, T., and Porteiro, F. M.: Cold-water corals landed by bottom longline fishery in the Azores, *J. Mar. Biol. Assoc. UK*, 92, 1547–1555, doi: 10.1017/S0025315412000045, 2012
9. Carreiro-Silva, M., Braga-Henriques, A., Sampaio, Í., Matos, V., Porteiro, F. M., and Ocaña, O.: *Isozoanthus primnoidus*, a new zoanthid species (Anthozoa: Hexacorallia) associated with the gorgonian *Callogorgia verticillata* (Anthozoa: Octocorallia) in the Azores, *ICES J. Mar. Sci.*, 68(2), 408–415, doi: 10.1093/icesjms/fsq073, 2011
10. Sampaio, Í., Ocaña, O., Tempera, F., Braga-Henriques, A., Matos, V., and Porteiro, F. M.: New occurrences of *Corallium* spp. (Octocorallia, Coralliidae) in the Central Northeast Atlantic, *Arquipélago, Life and Marine Sciences*, 26, 73–78, 2009

UNIVERSIDADE DOS AÇORES
SUMÁRIO

**AS COMUNIDADES DE CORAIS DE ÁGUAS FRIAS NOS AÇORES:
DIVERSIDADE, HABITAT E CONSERVAÇÃO**

por Andreia Filipa Domingues Braga Henriques

Os corais de águas frias constituem importantes e abundantes componentes estruturais dos habitats bentónicos do mar profundo, criando condições favoráveis para uma maior abundância e variedade de invertebrados e peixes, muitos deles de elevado valor comercial. Contudo, o conhecimento acerca da diversidade taxonómica e dos padrões de distribuição desses organismos frágeis e de crescimento lento é escasso e fragmentado, o que dificulta a implementação de medidas de conservação e gestão espacial eficazes na região dos Açores (capítulo 1).

Neste estudo foi feita uma compilação exaustiva de todos os registos disponíveis referentes aos principais grupos de corais de águas frias construtores de habitat – Alcyonacea, Antipatharia, Scleractinia e Stylasteridae – de modo a determinar a diversidade, distribuição e estrutura espacial das suas comunidades na Zona Económica Exclusiva (ZEE) dos Açores (capítulo 2). A base de dados resultante compreende 2501 registos obtidos em expedições oceanográficas históricas e noutras fontes, assim como dados não publicados provenientes de capturas acidentais com o palangre de fundo da frota açoriana. Este inventário taxonómico encontra-se bastante completo para os habitats já explorados compreendendo um total de 164 espécies (79 alcionáceos, 58 escleractíneos, 18 antipatários and 9 stilasterídeos), nove das quais documentadas pela primeira vez nos Açores. O número de espécies aparentemente endémicas é reduzido (14 % do total observado) e a sua ocorrência é apenas suportada em parte por uma amostragem consistente. Os mapas de distribuição produzidos a uma escala regional evidenciaram a existência de uma abundância considerável de áreas ricas em corais dispersas pelo arquipélago (> 20 espécies, max. 73), as quais são indicadoras de ecossistemas marinhos vulneráveis. A diversidade específica é mais elevada entre os 300 m e os 900 m de profundidade e em particular nos bancos de pesca situados dentro das 100 milhas da ZEE. As comunidades de corais presentes entre os 100–1500 m de profundidade exibem estratificação geográfica e batimétrica, evidenciando uma clara transição na composição faunística entre os 600–1000 m.

O monte submarino Condor de Terra é um importante banco pesqueiro situado aproximadamente a 10 milhas a sudoeste da Ilha do Faial e encontra-se temporariamente interdito à pesca para estudos científicos (capítulo 3). A ocorrência e distribuição das comunidades de corais de águas frias foi aqui investigada com base em transectos de vídeo efetuados com veículos submersíveis de operação remota (ROVs) entre os 185 m e os 1100 m de profundidade, procedendo-se assim à validação visual de parte dos resultados obtidos no capítulo 2 em termos de diversidade e estrutura faunística espetável. Os dados recolhidos foram posteriormente complementados com registos de capturas acessórias de corais com palangre de fundo (185–1269 m), para estimar a diversidade destes organismos na área de estudo. A fauna de corais era composta maioritariamente por indivíduos da ordem Alcyonacea (47.5 %), os quais eram também os principais construtores de habitat em conjunto com as esponjas (Porifera). Não foram observadas estruturas de recife de corais duros (Scleractinia) e os grupos Actiniaria, Ceriantharia e Zoantharia estavam pouco representados. Foi verificada uma clara alteração da composição faunística das comunidades de corais ao longo do perfil batimétrico de amostragem. No cume do monte submarino foram encontradas comunidades dominadas por alcionáceos: *Dentomuricea* aff. *meteor* (até 0.95 m de altura), *Viminella flagellum* (até 1.5 m), assim como outras espécies de tamanho bastante mais reduzido (< 20 cm), isto é, *Bebryce mollis*, *Schizophytum echinatum*,

Villogorgia bebrycoides e *Nicella granifera*. Por outro lado, eram as gorgónias de tamanho médio pertencentes à espécie *Candidella imbricata* e os corais solitários *Leptopsammia formosa* e *Caryophyllia* sp.1 que caracterizavam a comunidade encontrada a maior profundidade (970–1010 m). Foi verificado que o tipo de fundo (arenoso vs. rochoso) influenciava a distribuição espacial dos corais. As comunidades acima dos 471 m revelaram sinais claros de pressão por parte da atividade pesqueira com palangre de fundo (presença de linhas, chumbos e bóias presas em corais ou estruturas rochosas), verificando-se danos físicos em 39.7 % das colónias. Foram também observadas colónias desprovidas de tecido por ação de predadores e não por contacto físico com aparelhos de pesca. A descoberta de uma considerável diversidade de biótopos de corais numa área reduzida de amostragem visual, vem demonstrar a riqueza ecológica dos ecossistemas marinhos vulneráveis presentes na região dos Açores, corroborando os resultados do capítulo 2, e alertando para a necessidade urgente da sua documentação e proteção.

As interações biológicas entre corais e fauna associada foram também alvo de estudo nesta tese. A observação de vídeo contínuo de diversas campanhas oceanográficas no arquipélago dos Açores permitiu identificar vários caranguejos *Paromola cuvieri*, uma espécie comercial de tamanho considerável, sobretudo em habitats de conservação prioritária pela OSPAR, nomeadamente jardins de corais e agregações de esponjas (capítulo 4, secção 4.1). A maioria destes animais transportava espécimes vivos de gorgónias e esponjas sobre a caparacha auxiliados pelo quinto par de pereiópodes. Este tipo de comportamento foi investigado através da análise de vários transectos visuais realizados com os veículos submersíveis ‘LULA500’ (FRN) e ‘LUSO’, verificando-se que a seleção do material transportado era baseada em diversos fatores de ordem morfológica e química (forma, tamanho, peso e palatabilidade), e não só pela abundância dos mesmos no fundo marinho. Durante a descrição dos habitats foram identificados mais de 59 taxa na categoria de megafauna sésil, incluindo esponjas, hidrários, corais, braquiópodes, crinóides e ostras, o que reforça a importância ecológica deste tipo de ecossistemas como promotores de biodiversidade marinha e habitat bentónico.

O stilasterídeo *Errina dabneyi* consiste numa das espécies de corais mais frequentemente observadas no mar profundo dos Açores. Estes organismos formam estruturas calcárias complexas de considerável relevo, apresentando por isso um maior grau de vulnerabilidade à pesca de fundo (capítulo 4, secção 4.2). Os resultados demonstraram que estes organismos são colonizados por uma variedade de pequenos invertebrados, destacando-se uma espécie de gastrópodes pouco estudada pertencente à família Pediculariidae. De modo a descrever em detalhe estes organismos e caracterizar o tipo de associação simbiótica foram examinadas 43 colónias de *E. dabneyi* provenientes de capturas acessórias da pesca com palangre de fundo (201–1097 m). A associação gastrópode–stilasterídeo foi também documentada no seu ambiente natural durante transectos visuais bentónicos realizados com o submarino tripulado ‘LULA500’ na encosta sul do Canal Faial–Pico (450 m). O grau de incidência desta espécie no coral hospedeiro é elevado (69.8 %), tendo-se registado uma abundância máxima de 223 indivíduos por colónia. Após a sua identificação como *Pedicularia sicula* procedeu-se a uma análise morfológica da concha que permitiu descrever esta espécie nas diferentes fases de crescimento, dando-se particular atenção à protoconcha. As observações efetuadas permitiram detetar um grau de plasticidade da concha elevado, as quais estavam fixas aos ramos do stilasterídeo. A natureza da associação entre *E. dabneyi* e *P. sicula* parece ser um caso típico de parasitismo, em que o hospedeiro disponibiliza abrigo e alimento ao parasita, que por sua vez causa dano evidente no hospedeiro.

Esta tese afigura-se como uma valiosa contribuição para dar continuidade ao desenvolvimento de estratégias eficazes de conservação dos ecossistemas marinhos vulneráveis dos Açores. Os novos dados taxonómicos e ecológicos aqui apresentados

permitiram enriquecer o conhecimento existente em corais de águas frias que existem em montes submarinos e encostas de ilhas oceânicas do nordeste Atlântico. Procurou-se assim reforçar a sua importância para a manutenção da biodiversidade marinha e vulnerabilidade face às ameaças antropogénicas atuais, como por exemplo a pesca de fundo, e em crescente expansão, a exploração de recursos minerais no leito marinho (capítulo 5).

UNIVERSITY OF THE AZORES
SUMMARY
**COLD-WATER CORAL COMMUNITIES IN THE AZORES:
DIVERSITY, HABITAT AND CONSERVATION**
by Andreia Filipa Domingues Braga Henriques

Cold-water corals (CWCs) are widely considered as important, and abundant, structural components of deep-sea benthic habitats, enhancing local abundance of variety of fish and invertebrate species, many of which are commercially valuable. Yet, current knowledge of the taxonomic diversity and distribution patterns of these vulnerable, slow-growing organisms is scarce and fragmented, limiting the effectiveness of spatial management and conservation measures in the Azores region (chapter 1).

An exhaustive compilation of records for the most representative groups of habitat building corals – Alcyonacea, Antipatharia, Scleractinia and Stylasteridae – available until the present day was conducted to assess the diversity, distribution, and spatial structure of coral assemblages in the Azores Exclusive Economic Zone, EEZ (chapter 2). The resulting database comprises 2501 entries concerning historical oceanographic expeditions and other sources, as well as unpublished data from bottom longline bycatch of the Azorean commercial fleet. The taxonomic inventory appears to be fairly complete for the explored habitats accounting for 164 species (79 alcyonaceans, 58 scleractinians, 18 antipatharians and 9 stylasterids), nine of which were for the first time recorded in the region. Very few apparent endemics were found (14 %), and only in part supported by consistent sampling. Regional distribution maps showed many coral hotspots, widespread throughout the archipelago (> 20 species, max. of 73), which are indicative of coral-associated vulnerable marine ecosystems. Coral diversity is particularly high between 300 and 900 m depths, in areas recognized as traditional fishing grounds within the 100-mile limit of the EEZ. The composition of coral assemblage shows significant geographical structure among longitudinal sections of the study area at comparable depths (100–1500 m), showing a clear transition between 600–1000m depths.

Located just ten miles to the southwest of Faial island (Azores, NE Atlantic), the Condor de Terra Seamount has been an important fishing ground during the last few decades and is now temporarily closed to fisheries for research purposes. The presence of CWC assemblages was investigated based on video surveys undertaken with remotely-operated vehicles in Condor de Terra Seamount at depths between 185 m and 1100 m (chapter 3). Coral bycatch records from bottom longline fishing (185–1269 m) were combined with ROV data to estimate species diversity. Alcyonacea is the best-represented group (47.5 %) and the most important habitat-forming structures together with Porifera. No live or dead massive reefs were observed, and actiniarians, cerianthids and zoanthids were poorly represented. Changes in coral faunal composition were associated with substratum type (soft vs. hard bottoms) and depth-related gradients. The alcyonaceans *Dentomuricea* aff. *meteor* (up to 0.95 m height) and *Viminella flagellum* (up to 1.5 m) along with other small-sized species (< 20 cm) such as *Bebryce mollis*, *Schizophyllum echinatum*, *Villogorgia bebrycoides* and *Nicella granifera*, comprised the dominant coral fauna at the seamount summit. The deepest coral community occurred at depths between 970–1010 m and consisted of medium-sized gorgonians of *Candidella imbricata* together with the solitary corals *Leptopsammia formosa* and *Caryophyllia* sp.1. Signs of longline fishing pressure were documented in coral assemblages occurring above 471 m depth, including lines, plastic ropes, buoys and cement weights snagged or entangled on high relief structures and corals. Mechanical injury was recorded in 39.7 % of the colonies observed. Colonies with partly-exposed axes (free of polyps and coenenchyme) also occurred, resulting from the feeding activity

of invertebrate epibionts rather than mechanical injury. Given that such a small area was surveyed, the existence of several distinct coral-dominated biotopes provides evidence of a wealth of vulnerable marine ecosystems in the Azores region. These findings corroborate with the results presented in chapter 2, and call for the urgent documentation and protection of those ecosystems.

Biotic interactions hosted by coral communities were also addressed in this thesis. The set of visual surveys undertaken during several oceanographic campaigns revealed the presence of several crabs *Paromola cuvieri*, a large commercial species, inhabiting priority habitats of conservation importance under OSPAR, in particular coral gardens and sponge aggregations (chapter 4, section 4.1). Of these, most were carrying live gorgonian and sponge specimens over their carapace with the help of the fifth pereopods. Carrying behaviour was described based on video footage collected by the submersible vehicles 'LULA500' (FRN) and 'LUSO' to investigate if surrounding habitat influences the selection of carried objects. The process of object selection was seen to be more complex than previously thought, and factors such as morphology, size and weight and also palatability of objects seemed to be more important than their availability in the seafloor. Diverse sessile megafauna were recorded (> 59 taxa), including sponges, hydroids, corals, brachiopods, crinoids and oysters, which emphasises the ecological importance of these ecosystems as sources of benthic habitat and promoters of marine biodiversity.

The stylasterid *Errina dabneyi* is one of the most abundant corals in deep-water benthic habitats of the Azores. This species is particularly vulnerable to bottom fishing because it creates complex carbonate structures of high relief. Results show that they host a rich fauna of small invertebrates, including a poorly known gastropod species belonging to the family Pediculariidae (chapter 4, section 4.2). Forty-three colonies of *E. dabneyi* obtained as bycatch from bottom longline fishing (201–1097 m) were examined to identify the gastropods to species-level and to determine the nature of the symbiotic relationship. *In situ* observations of the association were made during benthic surveys of the southern slope of the Faial-Pico Channel (450 m) using the manned submersible 'LULA500'. The stylasterid-associated gastropods were identified as *Pedicularia sicula*. The incidence of this species on *E. dabneyi* was high (69.8 %), with a maximum abundance of 223 individuals per colony. A detailed description of *P. sicula* is provided based on shell morphological data at different growth stages with particular emphasis on the protoconch-specific characters. The pediculariids exhibited a high degree of plasticity and produced evident traces on the stylasterid skeletons at their fixation points, suggesting that they are ectoparasites and not predators of *E. dabneyi*.

This thesis constitutes a valuable contribution to the ongoing development of efficient conservation policies for coral-associated vulnerable marine ecosystems of the Azores (chapter 5). The results presented herein expand our understanding on cold-water coral communities over vast insular slope habitats and seamounts of the northeast Atlantic, reinforcing their ecological importance for the sustainability of marine biodiversity as well as vulnerability to current (e.g. bottom fishing) and emergent (e.g. seabed mining) anthropogenic threats.

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CHAPTER 1

General introduction

Cold-water corals (CWCs) have been a topic of much interest to marine researchers, conservationists, policy makers and stakeholders, since their ecological importance as abundant members of deep-sea benthic communities were brought to light (Freiwald et al., 2004; Roberts et al., 2006). Even though first reports on CWC occurrences date from more than two centuries ago (Forbes and Godwin-Austen, 1859), evidence of their ocean-wide distribution at unexpected depths (> 8000 m for antipatharians) was only recognised over the last two decades, thanks to advanced underwater surveys and higher access to the deep sea. Those findings greatly magnified the value of CWC ecosystems on a global scale and lead to increased interdisciplinary research on this theme (Watling and Risk, 2002; Freiwald and Roberts, 2005; Miller et al., 2009; Roberts et al., 2009; Mienis et al., 2014).

In this scenario, the region of the Azores was not an exception and vulnerable marine ecosystems (VMEs) dominated by rich gorgonian assemblages were also discovered during exploratory video surveys in the vicinity of Faial Island (Braga-Henriques et al., 2006). By that time, the majority of literature referred to species descriptions (e.g., Studer, 1890, 1891, 1901; Zibrowius, 1980; Zibrowius and Cairns, 1992; Ocaña et al., 2007) coupled with a few *in situ* observations made in 1969 with the French submersible Archimède (CNEXO, 1972). Despite the increasingly strong evidence that many coral species were being towed up by bottom longline gears (see Chapter 2: Table 2.4, Fig. 2.5), those new surveys revealed well-preserved assemblages, prompting the need for sustainable management of those ecosystems by conservation managers and policy makers. Furthermore, it was widely recognized that fishing activities were expanding either to deeper grounds or unexploited areas (e.g. seamounts) due to exhaustion of commercial fish stocks at inshore areas (Gordon, 2003; Morato et al., 2006). Thus, and given the raised concern of rapid habitat destruction, it was urgent

to explore the diversity and map the extent of CWC ecosystems in this vast region that were to date largely undescribed.

In this chapter I present a review of the published information relevant to this thesis, starting by defining the term ‘cold-water coral’ and discussing the current status of CWC taxonomic classification. Next, I briefly document what is known about morphology, biogeography, growth rates and longevities, associated fauna and symbiotic organisms of CWC species. I also include a sub-section on threats and conservation measures where special attention is given to the impacts of fishing on VMEs and describe global actions to protect those habitats. Finally, I summarise the rationale, structure and aims of this thesis.

1.1 DEFINITION AND CLASSIFICATION

Cold-water corals, also commonly referred as deep-sea or deepwater corals, are cnidarians of the classes Anthozoa and Hydrozoa comprising seven major taxonomic groups (reviewed by Roberts and Cairns, 2014): i) order Scleractinia Bourne, 1900 (stony corals, hard corals, cup corals, true corals), ii) order Zoanthidea Gray, 1832 (in part; zoanthids, gold corals), iii) order Antipatharia Milne-Edwards and Haime 1857 (black corals, thorny corals, wire corals), iv) subclass Octocorallia (soft corals, gorgonians, sea fans, sea whips, sea feathers, sea pens, precious corals, golden corals, bamboo corals, leather corals, horny corals), v) family Stylasteridae Gray, 1847 (lace corals, “hydrocorals”), vi) family Hydractiniidae L. Agassiz, 1862 (in part, longhorn hydrozoans), and vii) family Milleporidae Fleming, 1828 (fire corals, “hydrocorals”). CWCs may be skeleton-less or possess either mineral (i.e. calcium carbonate – aragonitic and/or calcitic) or horn-like proteinaceous skeletons (Cairns, 2007).

Anthozoan corals are divided into two groups, Octocorallia and Hexacorallia, based on two types of body construction (Daly et al., 2007). While most hexacorallians present hexamerous symmetry, the octocorallians are octamerous bearing polyps with eight unpaired mesenteries that give rise to eight pinnate tentacles. However, it should be noted that hexacorallians could also have polyps with eight- or ten-part symmetry. The scleractinians, zoanthids and antipatharians display hexamerous symmetry and therefore are placed in Hexacorallia. Most interpretations of phylogenetic relationships within Hexacorallia support monophyly of each of the extant orders (i.e. Actiniaria, Antipatharia, Corallimorpharia, Scleractinia and Zoanthidea) with the exception of

Ceriantharia (tube anemones) that should be elevated to subclass (Daly et al., 2007 and references therein; Stampar et al., 2014).

Taxonomic classification at ordinal and familial-level in the Octocorallia are widely recognized to be problematic. The scarcity of good discriminating morphological characters, intraspecific variation (e.g., colony shape, sclerite forms) and frequent homoplasy (convergences, parallelisms, and reversals) are indicated as greatly contributing to this discrepancy among other major groups of cnidarians (Bayer, 1981a; Williams, 1997). Currently in a state of flux with many species being re-described and synonymised, Octocorallia have long been subject of several attempts to understand their taxonomy and phylogenetic relationships by modern taxonomists (Bayer, 1981b; France et al., 1996; Berntson, 2001; Won et al., 2001; Sánchez et al., 2003; McFadden et al., 2006, 2010). Throughout most of the twentieth century, Octocorallia was divided in six orders (Hickson, 1930), but the classification presently in use consists of Bayer's three-order system (Table 1.1): Alcyonacea (soft corals and gorgonians), Helioporacea (blue corals) and Pennatulacea (sea pens). Bayer (1981b) combined the historical orders Alcyonacea, Gorgonacea, Stolonifera, and Telestacea of Hickson's classification into a single order, Alcyonacea, due to the existence of intermediate forms linked to each of these groups that rule out any pithy rank description. For taxonomic usefulness, Alcyonacea is further sub-divided into discrete subordinal groups based on colony organization and skeleton composition (if present), i.e., Alcyoniina, Calcaxonia, Holaxonia, Protoalcyonaria, Scleraxonia and Stolonifera (Bayer, 1981b; Grasshoff, 1999). Nonetheless, it is broadly acknowledged that except for gorgonians suborders Holaxonia and Calcaxonia (Grasshoff, 1999), morphological synapomorphies still need to be identified within Alcyonacea (Fabricius and Alderslade, 2001; McFadden et al., 2006, 2010).

1.2 GENERAL MORPHOLOGY

As mentioned above, corals can exhibit a wide range of morphologies and discrimination between species based on gross external form is often a true challenge, in particular when single video footage is available. Here I will focus primarily on the deep-sea groups most commonly observed in the Azores.

Table 1.1 Current higher taxonomic classification of Octocorallia highlighting families that possess coral representatives occurring at depths below 200 m (adapted from Bayer, 1981b; McFadden et al., 2006). Square brackets are used to represent taxa without taxonomic significance.

Taxonomic group	Distinguishing characters	Family
Order ALCYONACEA		
[Group Stolonifera]	Soft corals with polyps united basally by stolons that may fuse to form ribbons or thin membranes	Clavulariidae
[Group Alcyoniina]	Soft corals lacking an axial skeleton	Alcyoniidae Nephtheidae
[Group Scleraxonia]	Gorgonians with an axial skeleton (or layers) composed of sclerites. Colonies with an axis or internal axial-like layer composed mainly of sclerites (unfused or fused with calcite)	Anthothelidae Briareidae Coralliidae Paragorgiidae Parisididae Subergorgiidae
[Suborder Holaxonia]	Gorgonians with an organic central axis with varying amounts of calcareous material deposited in loculi; axes with very little calcareous material are described as “woody”	Acanthogorgiidae Gorgoniidae Plexauridae
[Suborder Calcaxonia]	Gorgonians with a solid axis composed of large amounts of non-scleritic calcareous material	Chrysogorgiidae Ellisellidae Isididae Primnoidae
[Group Protoalcyonaria]	Solitary polyps	
Order HELIOPORACEA*	Corals that produce calcified skeletons of aragonite, an exclusive feature among other octocorallians	Lithotelestidae
Order PENNATULACEA	Corals that axial polyp differentiated into basal peduncle and distal rachis	Anthoptilidae Chunellidae Echinoptilidae Funiculinidae Halipteridae Kophobelemnidae Pennatulidae Protoptilidae Scleroptilidae Stachyptilidae Umbellulidae Veretillidae Virgulariidae

*This order comprises just two families: Helioporidae Moseley, 1876 (i.e. the shallow-water coral *Heliopora coerulea*) and Lithotelestidae Bayer and Muzik, 1977.

1.2.1 Octocorallia Haeckel, 1866

The subclass Octocorallia is the most species-rich group, including over 3000 extant species (Cairns, 2007; Daly et al., 2007). With the exception of the sediment-dwelling *Taiaroa tauhou* (family Taiaroidae: Bayer and Muzik, 1976), all species are colonial (Bayer et al., 1983) and the vast majority is common in deep waters (ca. 2325 species occur at depths greater than 50 m; Roberts and Cairns, 2014). Colonial organization is primarily based on two types of growth (Bayer, 1973; Bayer et al., 1983): (1) monopodial, where colony grows upward maintaining a distinct main axis on which the new polyps bud, creating lateral branches (e.g. *Metallogorgia melano-trichos*); and (2) sympodial, where a polyp buds one or two new polyps, thus displaying a zig-zag or spiral arrangement (e.g. *Chrysogorgia quadruplex*). When exhibited growth patterns do not fall into any of these categories it is termed “irregular branching” (e.g. *Eunicella*).

Morphological diversity of deep-sea octocorals includes an extraordinary variety of colony shapes (Fig. 1.1) such as capitate (e.g. *Anthomastus*), stolonate (e.g. *Cornularia*, *Clavularia*), bushy (e.g. *Acanella arbuscula*), flagelliform (e.g. *Viminella flagellum*), arborescent (e.g. *Paragorgia*), pinnate (e.g. *Callogorgia verticillata*) and pseudosolitary (e.g. *Umbellula*). The pennatulaceans, for instance, can be readily distinguished due to their unique appearance, i.e. colonies consisting of a single substantial primary polyp with a proximal muscular peduncle (Bayer, 1973). However, at familial-level these show an array of morphological combinations based on secondary polyp arrangement around the rachis (the polypiferous part). Williams (2011) throughout its recent review estimates over 200 valid species arguing that the growth forms exhibited by this group are remarkably diverse.

Primnoidae is the fourth largest octocorallian family and generally a group easily recognized by examination of the polyp calycular architecture ornamented with scale-like sclerites (Fig. 1.2). Colony forms may again be considerably variable even within a genus, as in *Narella* (dichotomously branched, pinnate, or unbranched; Fig. 1.2A–B), constraining the use of this morphological character in phylogenetic analyses due to limited discriminatory power (Cairns and Bayer, 2008: Table 1; Cairns and Bayer, 2009). Moreover, there is evidence that the branching structure can vary with growth stage in octocoral species (see Mosher and Watling, 2009: *M. melano-trichos*). As such, regardless the usefulness of colony shape to key out taxa, most species can be only distinguished by microscopic examination of their sclerites. These microscopic calcite crystals of various shapes and sizes may be found within the coenenchymal tissue (Bayer et al., 1983) and

seem to play an important ecological role at providing flexibility or rigidity to colonies as well as restricting contiguous sclerite movement (Lewis and Wallis, 1991).

Another aspect that should be also emphasised is that octocorals show a wide range of sizes with individuals varying from a few centimetres as in family Clavulariidae Hickson, 1894 (Bayer, 1981b), to several metres in height such as in families Primnoidae Milne Edwards, 1857 (up to 2 m), Paragorgiidae Kükenthal, 1916 (up to 8 m, Sánchez, 2005: Fig. 6), Chrysogorgiidae Verrill, 1883 or Isididae Lamouroux, 1812 (Watling, 2007). The highest gorgonian ever recorded was recently found in the northwest Hawaiian Islands. It belongs to species *Iridogorgia magnispiralis* (Chrysogorgiidae) and is estimated to measure 5.7 m tall (Watling et al., 2013).

1.2.2 Scleractinia Bourne, 1900

Scleractinians range from solitary corals with only one calice such as *Stephanocyathus*, to colonial, polystomatous forms (Fig. 1.3). The defining character shared by all members of this order consists in the rigid aragonitic calcium carbonate skeleton (corallum) external to the soft tissues, where polyps can retract for protection (Daly et al., 2007). Most part of taxonomic identification to family and genus level relies on gross morphological characteristics of the corallum such as shape, septal arrangement (yes/no Pourtalès Plan) or presence/absence of columella (axial structure that projects from the middle of a calice). Detailed illustrations of most morphological characters used to discriminate scleractinians can be found in Cairns (1994: Figs. 1 and 2) and Cairns and Kitahara (2012).

Recent estimates of species richness for this order accounted for 1488 scleractinians, of which 622 (41.8 %) occur at depths greater than 50 m (Roberts and Cairns, 2014). Even though one of the best-known azooxanthellate scleractinians, *Lophelia pertusa*, may create extensive reef frameworks in the northeast Atlantic reaching up to 30 m in height (e.g., Wilson, 1979b; Freiwald et al., 2002), most of these are solitary (519 species). Many are free-living (e.g. *Flabellum* [*Ulocyathus*] *alabastrum*), a few show unattached corallum and base (e.g. *Eguchipsammia*, see Appendix E: Tempera et al., 2014), but the majority is rigidly attached to hard substrates (e.g. *Caryophyllia* [*Caryophyllia*] *atlantica*).

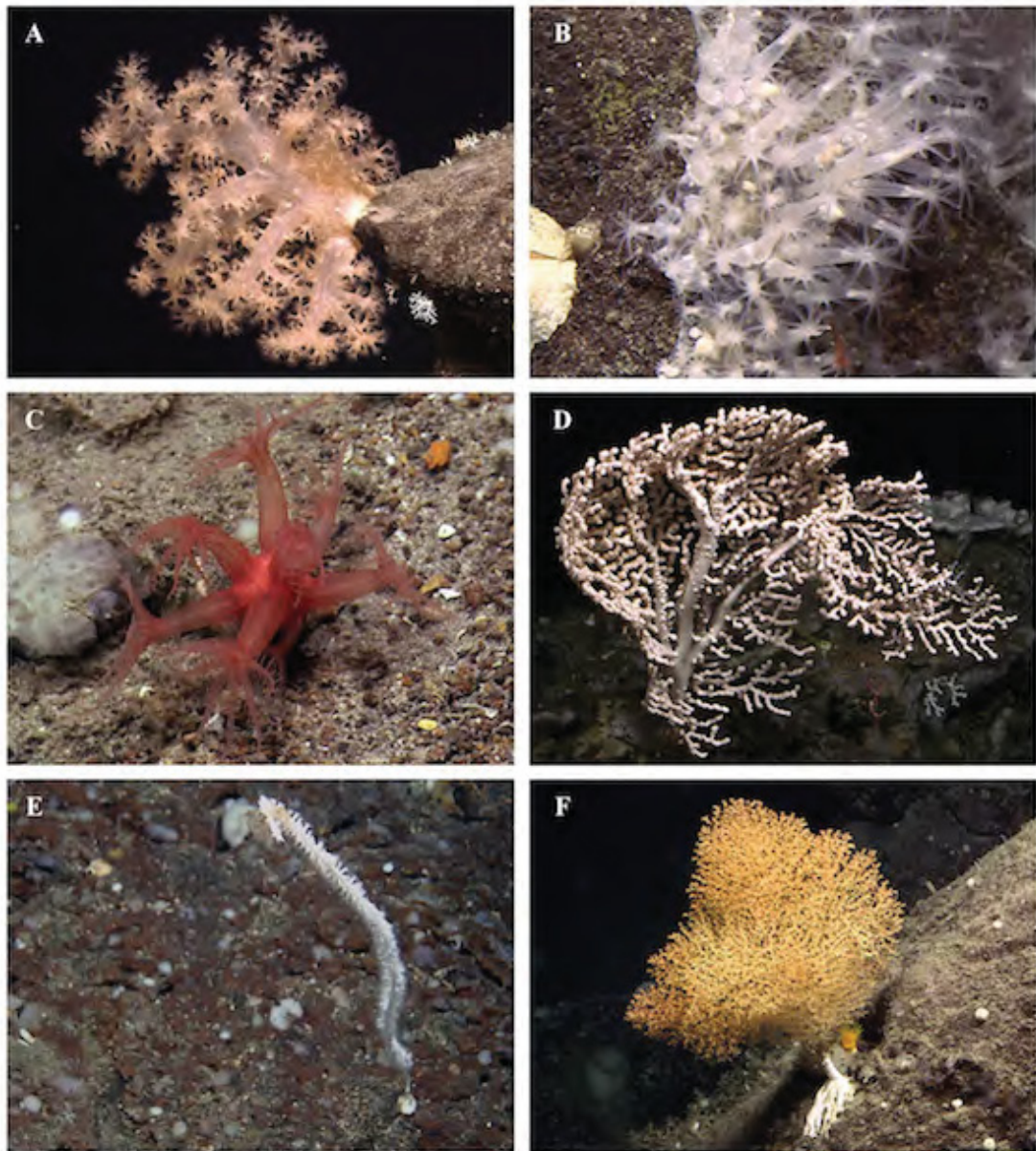


Figure 1.1 Octocorals. (A) Upright growth of an arborescent nephtheid coral that is extending off a vertical cliff and whose distinct stalk is clearly noticeable (895 m depth, southern slope of Pico Island, Azores); (B) A white stoloniferous octocoral at 895 m depth on the southern slope of Pico Island; (C) The soft coral *Anthomasthus* sp. at 700 m depth recorded off Faial Island slope, Azores; (D) The bubblegum coral *Paragorgia johnsoni* (\approx 60 cm in height) displaying robust branches with soft clumps (606 m depth, off Faial Island slope); (E) *Viminella flagellum*, members of this species exhibit whip-like branches with little to no ramification (575 m depth, Dom João de Castro Seamount, Azores); and (F) The bamboo coral *Acanella arbuscula* showing its root-like holdfast at 869 m depth on the southern slope of Pico Island. Images A–D and F courtesy of Rebikoff-Niggeler Foundation. Image E courtesy of Portuguese Task Group for the Extension of the Continental Shelf (EMEPC). Taxonomic identification provided by A. Braga-Henriques.

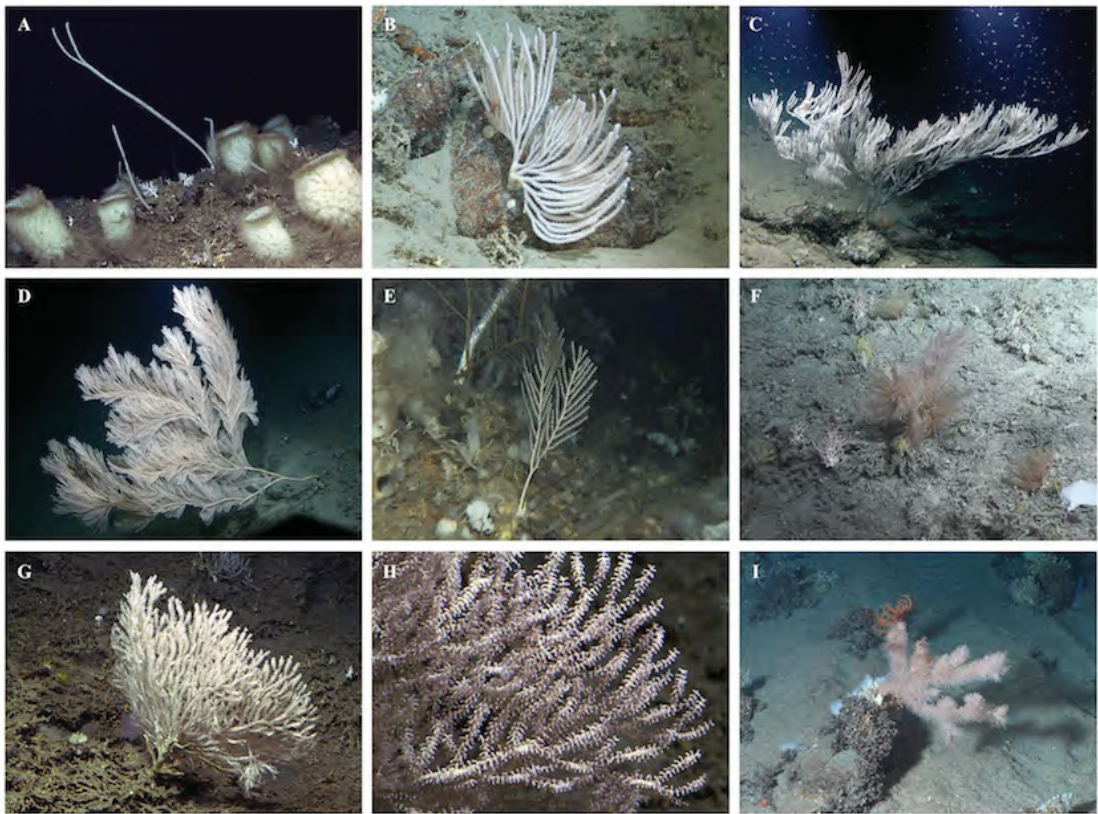


Figure 1.2 Primnoid corals (Alcyonacea). (A) Aggregation of *Narella verlyusi* colonies and *Pheronema carpenteri* sponges (742 m depth, southern slope of Pico Island, Azores); (B) A *Narella bellissima* colony showing the dichotomous branching in a lyriform pattern at 712 m depth on Douarnenez Canyon (Bay of Biscay); (C) The fan-shaped *Paracalyptophora josephinae*, whose dichotomous branching and downward-facing polyps are characteristic of the species (370 m depth, southern slope of Faial Island, Azores); (D) A large *Callogorgia verticillata* at 490 m depth recorded on the southern slope of Faial Island; (E) A young colony of *C. verticillata*, on which pinnate branching is clearly visible (426 m depth, Furnas de Fora, off São Miguel Island, Azores); (F) The gorgonian *Callogorgia americana* hosting several crinoids at 848 m depth on Logachev coral carbonate mound province (northwest coast of Ireland); (G) An adult colony of *Candidella imbricata* where is visible the highly calcified axis (946 m depth, southern slope of Pico Island); (H) Close-up of *C. imbricata* showing the dichotomous branching in one plane as well as the non-retractile polyps, the latter characteristic of the family; and (I) The bottlebrush-shaped *Thouarella (Euthouarella) cf. grasshoffi* with a bright orange brisingid starfish at 1560 m depth on Lampaul Canyon (Bay of Biscay). Images A, C, D, G and H courtesy of Rebikoff-Niggeler Foundation. Images B and F taken during the 2011 BobEco cruise, RV *Pourquois Pas?*, courtesy of French Research Institute for Exploitation of the Sea (IFREMER). Image E courtesy of EMEPC. Identification of invertebrate taxa provided by A. Braga-Henriques.

Representatives of the family Caryophylliidae Dana, 1846, the second most speciose among the Scleractinia (89 valid genera; Fig. 1.3A–B), range in size from small solitary forms < 5 mm in calicular diameter (e.g. *Caryophyllia* [*Caryophyllia*] *aspera*) to colonial structures such as the above-mentioned *L. pertusa*. The latter forms dendroid colonies firmly attached to the seabed showing irregular monostomaeous budding with many branches fusing together (Cairns and Stanley, 1982; Cairns and Kitahara, 2012). While the maximum size of a single colony of *L. pertusa* is about 1 m high and 1.5 – 2 m wide (Freiwald, 2003), the topographic elevations produced through time during reef development may be > 100 m tall (Hovland et al., 1997; Paull et al., 2000; Roberts et al., 2009). For an overview of the biogenic reef cycle regarding beginning, development, ‘retirement’ and re-colonisation of coral mound structures, see Roberts and Cairns (2014: Fig. 1).

The world’s largest known *Lophelia* reef, Røst reef complex, was discovered in 2002 at depths from 300 – 400 m along the continental edge off Norway and covers an area of approximately 35 – 40 km long and up to 3 km wide (Fosså et al., 2005). Here, species such as *Madrepora oculata* (family Oculinidae Gray, 1847) also contribute to reef growth (Sabatier et al., 2012: Fig. 1). This cosmopolitan scleractinian produces bushy colonies by extratentacular budding displaying fused branches (anastomosing) and calices without a palmar crown (Cairns and Kitahara, 2012). While in the northeast Atlantic *L. pertusa* is the dominant framework-forming species, *M. oculata* is predominant in some habitats of the Mediterranean region creating large thickets (Taviani et al., 2005; Freiwald et al., 2009; Vertino et al., 2010; Gori et al., 2013).

Other significant azooxanthellate scleractinians that form three-dimensional structures in deep-sea environments include *Oculina varicosa* (off the east coast of Florida: Macintyre and Milliman, 1970; Avent et al., 1977; Reed, 1980); *Solenosmilia variabilis* (Little Bahama Bank: Mullins et al., 1981; southern Tasmanian: Koslow et al., 2001); *Goniocorella dumosa* (New Zealand’s waters and adjacent banks: Squires et al., 1965; Cairns, 1995); *Enallopsammia profunda* (previously reported as *Dendrophyllia profunda*, Stetson et al., 1962); and *Bathelia candida* (Patagonian continental slope: Muñoz et al., 2012; Cairns and Polonio, 2013). Details on skeleton morphology for most of the above-mentioned reef-building species are well illustrated in Roberts et al. (2009).

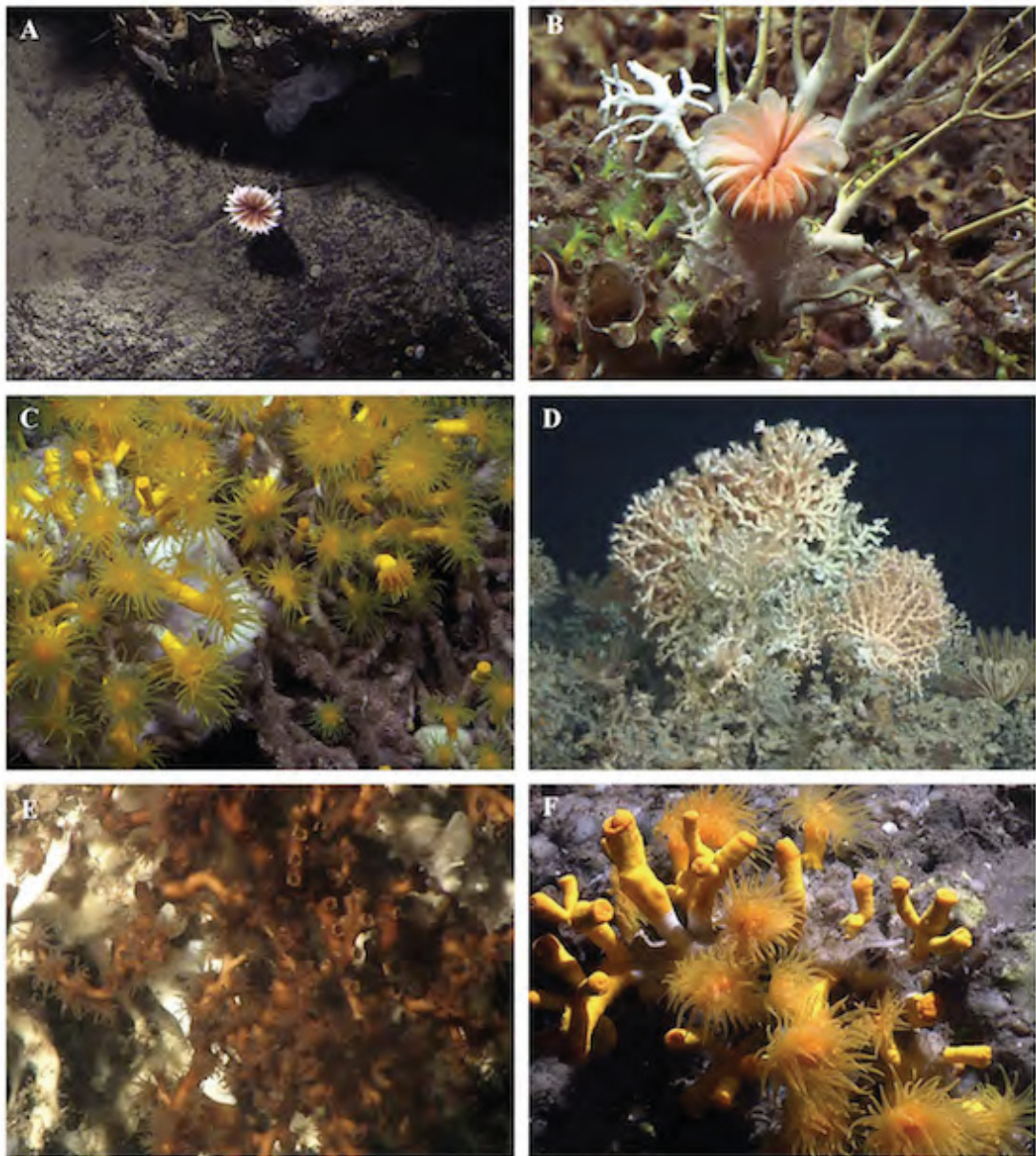


Figure 1.3 Scleractinian corals. (A) Calicular view of a solitary coral firmly attached to the hard substrate at 923 m depth on the southern slope of Pico Island, Azores; (B) The solitary coral *Desmophyllum dianthus* (Caryophylliidae) colonising the holdfast of an octocoral *Candidella imbricata* at 990 m depth on the southern slope of Pico Island; (C) Colonies of *Eguchipsammia* (Dendrophylliidae) showing the recumbent corallum at 280-300 m depth on top of a seamount-like feature in the Faial-Pico Channel (Azores), these were forming a monospecific coral reef; (D) Dead coral framework colonized by living thickets of *Lophelia pertusa* (upward growth) and *Madrepora oculata* (zigzag growth pattern) at 843 m depth on Croizic Canyon, Bay of Biscay; (E) A massive and bushy *Dendrophyllia alternata* (462 m, southern slope of Faial-Pico Channel); and (F) A *Dendrophyllia cornigera* colony firmly attached to the substrate \approx 400 m depth on the southern slope of Faial-Pico Channel. Images A–C, E and F courtesy of Rebikoff-Niggeler Foundation. Image D taken during the 2011 BobEco cruise, RV *Pourquois Pas?*, courtesy of IFREMER. Taxonomic identification provided by A. Braga-Henriques.

1.2.3 Antipatharia Milne-Edwards and Haime, 1857

Antipatharians are non-calcareous colonial animals known for having a characteristic flexible proteinaceous skeleton (black or dark brown) with very minute spines on its outer surface (Opresko, 2001; Daly, 2007; Fig. 1.4). These morphological attributes are responsible for the common names black coral and thorny coral. Due to structural and mechanical properties of the skeleton, several antipatharian species, like a few other anthozoans (e.g. *Corallium rubrum* – red coral, order Alcyonacea), have been subject to commercial harvesting for the manufacture of precious coral jewellery since the ancient Greek and Persian civilisations (Hickson, 1924; Tsounis et al., 2010). The coral material can be polished to an onyx-like lustre and due to its organic composition, can also be moulded while being heated (Kim et al., 1992). Driven by increased levels of exploitation, the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) decreed that antipatharians should be protected and, therefore, international trade has been regulated since 1981 in order to encourage the sustainability of wild populations (CITES, Appendix II).

In total, 44 genera and over 236 species of antipatharians are currently known worldwide (see Daly et al., 2007; Bo, 2008; MacIsaac et al., 2013). Of these, over 76 % are restricted to offshore deep-water environments, i.e. depths below 50 m (Roberts and Cairns, 2014). The corallum is covered with a narrow layer of tissue (coenenchyme) from which the polyps arise. These are contractile, but not retractile (i.e. they cannot be withdrawn into the oral cavity) and although could present six, ten or twelve complete, unpaired mesenteries, polyps always have six simple tentacles. Colony growth morphology can be highly variable as for instance in the family Schizopathidae Brook, 1889 emend. (Opresko, 2002), in which forms can be described as “bottle-brush” (e.g. *Parantipathes*), arborescent (e.g. *Lillipathes*), fan-shaped (e.g. *Stauropathes*), or even feather-like (e.g. *Bathypathes* and *Schizopathes*). Moreover, living colonies can display a wide range of tissue colours such as brown, red, orange, pink, green, yellow, white, and grey.

Deep-sea antipatharians are thus often confounded with gorgonians in their natural environment, which demands special attention particularly during the annotation of video transects. Furthermore, morphological changes with growth have also been documented in this group. For example, small/young colonies of the recently described species *Telopathes magna* resemble adult colonies of the genus *Bathypathes* (MacIsaac et al., 2013: Fig. 6B), which can lead to misidentifications if voucher

specimens are not available for posterior examination. Similarly, different branching patterns were observed on *Parantipathes larix* assemblages from Tyrrhenian Sea (Bo et al., 2014a). While smaller colonies possess a monopodial corallum without lateral branches, larger adult colonies have a highly ramified corallum displaying branches orientated upwards and downwards (up to 2.4 m tall and 19 branches).

Phenotypic plasticity is also a central problem in taxon distinction, particularly in branched species as it happens for octocorals (*Eunicella cavolinii*: Velimirov, 1976; Weinbauer and Velimirov, 1995), because there is empirical evidence that colony architecture can change in response to surrounding environmental conditions (Warner, 1977). Previous investigations on the fan-shaped species *Antipathes atlantica* in northwest Trinidad (off Venezuela) revealed that exposed colonies were more densely branched and had thicker stems than those living in sheltered habitats (Warner, 1981: Fig. 15). Indeed, most species can be only distinguished by microscopic examination of axial spines, which are of the order of one to ten millimetres in diameter. The examination of this feature is very important given that antipatharians lack any calcareous structures such as sclerites (octocorals) or spicules (sponges) on their soft tissues or axis. Examples of skeletal features, including axial spines, are provided in Appendix E for two antipatharian species with known distribution in the Azores: *Antipathella subpinnata* (de Matos et al., 2014a: Fig. 2) and *Heteropathes opreski* (de Matos et al., 2014b: Figs. 1 and 2).

Many classification schemes have been adopted over time for the order Antipatharia (Milne Edwards and Haime, 1857; Brook, 1889; Schultze, 1896; Roule, 1905; van Pesch, 1914), but presently six families are recognized: (1) Antipathidae, (2) Schizopathidae, (3) Cladopathidae, (4) Leiopathidae, (5) Myriopathidae, and (6) Aphanipathidae (Opresko, 2001, 2002, 2003, 2004, 2006). This taxonomic clarification has helped researchers to improve identifications, and consequently, avoid the continuing establishment of new species that quite often were no more than junior synonyms or young specimens of an already described species. Main diagnostic and descriptive features used in antipatharian taxonomy at the family-level include polyp structure (i.e., number and arrangement of mesenteries; size and shape of tentacles) and morphology of axial spines (Daly, 2007 and references therein).

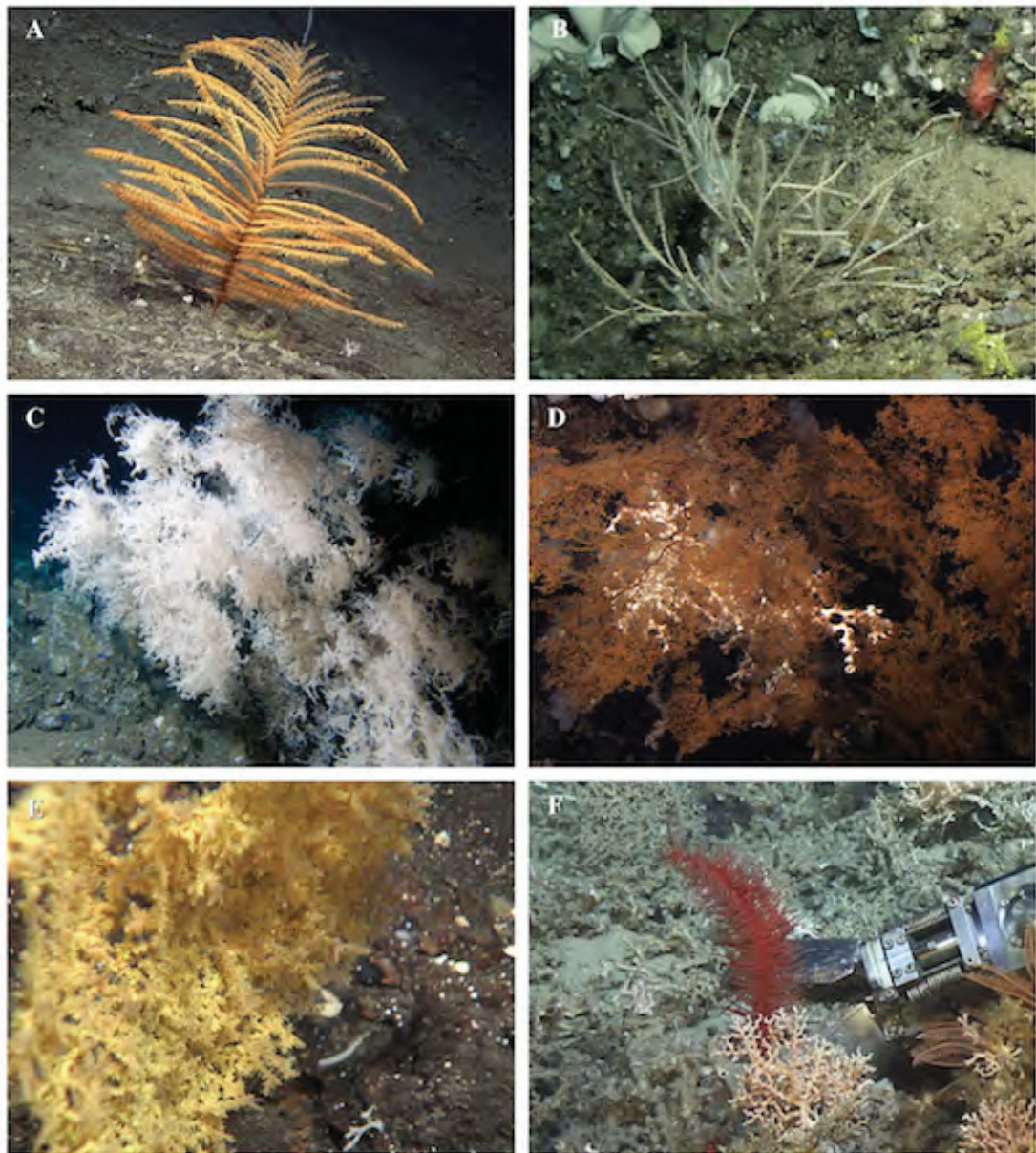


Figure 1.4 Antipatharian corals. (A) The bright orange *Bathypathes* sp.A showing the characteristic feather-like shape and primary pinnules in two lateral rows (907 m depth, southern slope of Pico Island, Azores); (B) The fragile *Antipathes* sp. with a corallum sparsely branched (424 m, eastern slope of Terceira Island, Azores); (C) An arborescent *Leiopathes* sp.A colony illustrating the irregular sympodial corallum and the lacking of pinnules (322 m, southern slope of Faial Island, Azores); (D) Another *Leiopathes* colony, however of a different species, found on a steep-walled habitat (962 m, southern slope of Pico Island); (E) Flabellate growth form of a large specimen of the Aphanipathinae subfamily (1116 m, slope of São Jorge Island, Azores); and (F) A *Parantipathes* sp. colony exhibiting the distinctive bottle-brush pinnulation pattern (812 m, Guilvinec Canyon, Bay of Biscay). Images A, C and D courtesy of Rebikoff-Niggeler Foundation. Images B and E courtesy of EMEPC. Image F taken during the 2011 BobEco cruise, RV *Pourquois Pas?*, courtesy of IFREMER. Taxonomic identification provided by A. Braga-Henriques.

1.2.4 Stylasteridae Gray, 1847

Stylasteridae is the second most speciose hydrozoan family comprising to date 249 valid Recent species with 89.6 % of these found at depths below 50 m (Bouillon et al., 2006; Roberts and Cairns, 2014). Members of this group are exclusively colonial bearing a delicate calcium carbonate skeleton (coenosteum), usually aragonitic, although a few species produce instead calcitic or partially calcitic skeletons (Cairns, 1983a; Cairns and Macintyre, 1992; Cairns, 2011). A thin layer of tissue covers the coenosteum, which texture differs between species such as linear-imbricate in specimens of the genus *Pliobothrus* (Fig. 1.5B) and reticulate-granular in *Errina dabneyi* (Fig. 1.5D).

Throughout the coenosteum, a number of openings named cyclosystems can be found. The spatial arrangement of the cyclosystems is a distinguishing feature used in species identification (Cairns, 1983a). Polyp morphology is much simpler than in anthozoans and internal mesenteries are absent. Three types of polyps with discrete functions can be found in stylasterids: the gastrozooids (feeding), the dactylozooids (defence and to support food uptake) and the gonophores (reproduction). As either female or male, colonies exhibit a strong sexual dimorphism of the skeletal ampullae (skeletal encasement of the gonophore), which is also used as a distinguishing character in Stylasteridae (Cairns, 1983a; 1992a).

Stylasterids usually form small colonies displaying uniplanar to slightly arborescent branching patterns and are often brightly coloured, e.g. orange, red, pink, blue, brown, or violet (Cairns, 2011). Conversely, species occurring in the Azores are all white or creamy-white (Fig. 1.5). As a diverse group of hard corals, the second most after Scleractinia, some species may also create dense coral biotopes of reef-like or two-dimensional habitat-forming structures firmly attached to the substrate (Ostarello, 1973; Miller et al., 2004; Roberts et al., 2009; Love et al., 2010).

An extreme case of stylasterid abundances was reported by Häussermann and Försterra (2007) in Central Patagonian, where they found large *Errina antarctica* colonies (over 40 cm in diameter) creating substantial and three-dimensional assemblages that covered areas of more than 10 km² at depths below 10 m. More recently, visual surveys in the Mediterranean Sea also showed high densities of *Errina aspera* (101.4 colonies /m²) revealing a predominance of small-sized colonies of 4.1 cm tall on average (Salvati et al., 2010). Besides the two above-mentioned species, 15 additional stylasterids possess habitat-building potential (Roberts et al., 2009): *Calyptraphora reticulata* (south of New Zealand), *Distichopora sulcata* (off Cuba),

Errinopora nanneca (Aleutian Islands), *Errinopsis reticulum* (southern South America), *Stenohelia concinna* (Galápagos), *Stylaster brochi* (Bering Sea), *Stylaster californicus* (off California), *Stylaster campylecus* (Aleutian Islands), *Stylaster cancellatus* (Aleutian Islands), *Stylaster densicaulis* (southern South America), *Stylaster eguchii* (circum-Antarctic), *Stylaster erubescens* (North Atlantic), *Stylaster filogranus* (Straits of Florida), *Stylaster miniatus* (South Carolina to Florida).

Worthy of note is the remarkable morphological similarity with the bryozoans, which prompted the erroneous placement of a few species in bryozoan genera. For example, *Lepidopora eburnea* was originally assigned to *Hornera eburnea* (Calvet, 1903) and *Pliobothrus symmetricus* to *Hornera gravieri* (Calvet, 1911). In some particular cases such as poor quality footage, stylasterid species may also resemble colonial scleractinians due to their prominent calcified skeleton. A series of publications by Cairns (1983a, 1983b, 1992a, 1992b) are a rich source of taxonomic information at providing dichotomous keys to genera, comprehensive descriptions of species and geographical distribution. Additionally, Zibrowius and Cairns (1992) present an excellent taxonomical revision of the northeast Atlantic and Mediterranean stylasterid fauna along with a key to the genera from the study area. An illustrated glossary of the terminology used in stylasterid taxonomy can also be found in Cairns (2011).

1.3 HABITAT

Studies focusing on diversity and distribution of cold-water corals have shown that these organisms can be found in all marine environments across the globe including continental shelves (Fosså et al., 2002; Watling and Auster, 2005; Le Guilloux et al., 2009; Arantes et al., 2009), offshore banks (e.g., Tissot et al., 2006; Wareham and Edinger, 2007; Murillo et al., 2011), canyons (e.g., Mortensen and Buhl-Mortensen, 2005; Baker et al., 2012; Morris et al., 2013; Gori et al., 2013; Brooke and Ross, 2014), fjords (e.g., Häussermann and Försterra, 2007), hydrothermal vent fields, oceanic island shelves (e.g., Heifetz, 2002), ridges (e.g., Molodstova et al., 2008; Mortensen et al., 2008; Morris et al., 2012), and seamounts (e.g., Matsumoto et al., 2005; Rogers et al., 2007; Etnoyer, 2010; Waller et al., 2011).

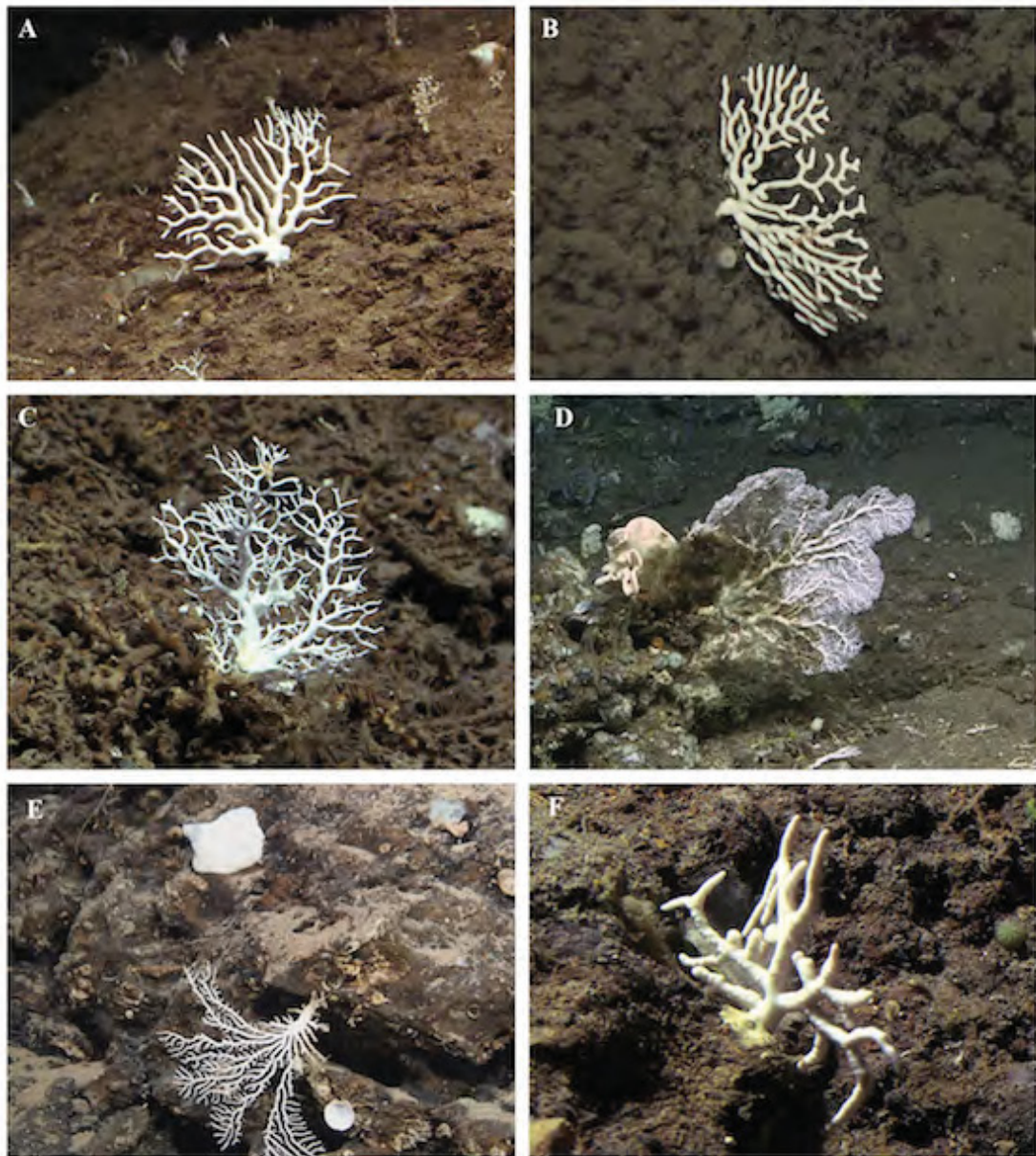


Figure 1.5 Stylasterid corals. (A) A small uniplanar colony and two young *Cryptthelia* colonies on its right at 990 m depth on the southern slope of Pico Island, Azores; (B) A *Pliobothrus* colony showing some of the characteristic features of the genus: uniplanar shape, robust and cylindrical branches that become more flattened along the branching plane (991 m depth, off São Jorge Island slope, Azores); (C) A young *Errina atlantica* colony showing the bushy growth pattern at 955 m depth on the southern slope of Pico Island; (D) A large fan-shaped colony of *Errina dabneyi* found on a current-exposed ridge at 460 m depth on the southern slope of Faial Island, Azores; (E) A stylasterid sp.1 colony extends off a wall at 893 m depth on the southern slope of São Jorge Island; (F) A stylasterid sp.2 colony showing robust branches at 858 m depth on the southern slope of Pico Island; Images A, C, D and F courtesy of Rebikoff-Niggeler Foundation. Images B and E courtesy of EMEPC. Taxonomic identification provided by A. Braga-Henriques.

They usually occur in dysphotic and aphotic zones, mainly on seabed features of pronounced topographic relief, and at current-exposed sites (Davies and Guinotte, 2011; Yesson et al., 2012; Tong et al., 2012). As suspension-feeders, nutrition relies on diverse food sources from particulate organic matter to zooplankton (Slattery et al., 1997; Orejas et al., 2003; Kiriakoulakis et al., 2005; Sherwood et al., 2005; Purser et al., 2010; Tsounis et al., 2010; Naumann et al., 2011) and, thus, by inhabiting these types of features, food supply is potentially enhanced (Mortensen et al., 2001; Thiem et al., 2006; Kiriakoulakis et al., 2007). Species with large individual polyps, such as many scleractinians, are more likely adapted to capture large and live preys than those corals harbouring smaller polyps, which is the case of most octocorals. Furthermore, accumulation of fine-grained sediments is avoided increasing early post-settlement survivorship of new recruits (Genin, 1986; Bryan and Metaxas, 2006; Lacharité and Metaxas, 2013).

Current evidence suggests that CWC ecosystems are comparable to shallow-water tropical reefs in richness and coral densities (Roberts et al., 2009). It is important to emphasize that almost 66 % of the global coral diversity, i.e. 3356 of all 5160 known species, is found in waters deeper than 50 m (Cairns, 2007; updated in Roberts and Cairns, 2014).

1.4 GROWTH RATES AND LONGEVITIES

Cold-water corals are deemed to be slow-growing organisms with long life spans (Roberts et al., 2006) which extension growth rates varies from 0.5 mm (Adkins et al., 2004: *D. dianthus* and *Enallopsammia rostrata*) to > 64 mm per year (Grigg, 1976: *Antipathes dichotoma*). The first attempt to estimate coral growth rate dates back to late 19th century when Duncan (1877) observed colonies of the scleractinian *L. pertusa* growing on trans-Atlantic telegraph cables (4 – 8 mm/yr⁻¹). Similarly, a few other authors inferred growth estimates for this species from artificial structures (5 – 7 mm yr⁻¹ in Wilson, 1979b; 26 mm yr⁻¹ in Bell and Smith, 1999; 26 ± 5 mm yr⁻¹ in Gass and Roberts, 2006). However, the methodology employed was likely to underestimate growth rates and overestimates age given that it was presupposed that age of largest colonies were as same as the age of the structures on which they had been found. Nowadays, a range of techniques with an acceptable level of precision is available to determine annual colony growth and age for a number of species, i.e. radioisotope

dating, growth ring counting, amino acid racemization dating and also time-series measurements (Table 1.2). Age estimates of gorgonian species are of the order of decades to hundreds of years, for which ^{14}C or ^{210}Pb decay rates are the most commonly chosen methodologies. For *Primnoa resedaeformis* (Primnoidae), one of the most often-reported gorgonians found off northern Europe, estimates range from 18 ± 4 years by means of growth ring counts (Sherwood and Edinger, 2009) to 700 ± 100 years using radiocarbon dating (Sherwood et al., 2006). The latter refers to a fossil specimen and represents the longest-lived octocoral yet dated. Nonetheless, the most impressive lifespan ever recorded was an antipatharian aged to 4265 ± 44 calendar years with a radial growth rate of 0.002 mm/yr^{-1} (Roark et al., 2009). The colony, identified as *Leiopathes* sp., was live-collected in Hawaii between depths of 400 and 500 m and it is thought to be the oldest living colonial invertebrate on record.

Coral growth rates may greatly depend on abiotic and biotic factors such as temperature, current, turbidity, ocean chemistry and food supply (e.g., Guinotte et al., 2006; Thiem et al., 2006; White et al., 2007; Dullo et al., 2008; Roberts et al., 2009). Therefore, interspecies variability as a response to environmental adaptation may highly influence estimates, even when following similar estimation methods. Radial growth of isidid gorgonians (also known as bamboo corals) increased linearly with ambient temperature ($2 - 5^\circ \text{C}$), but below 2°C was $10 - 15 \mu\text{m yr}^{-1}$, and above 5°C become more or less constant growing $165 \mu\text{m yr}^{-1}$ (Thresher, 2009). Aquaria measurements of *L. pertusa* showed that increased food supply was followed by high extension rates for colonies collected in Norway and Scotland respectively (Mortensen, 2001; Roberts and Anderson, 2002). Rogers (1999) also indicated faster growth rates for fragments maintained in the laboratory (up to 2.5 cm yr^{-1}). In the northern Gulf of Mexico, Brook and Young (2009) used transplant units of *L. pertusa* fragments, previously stained with Alizarin red, to assess species growth. They found an average linear growth rate of 3.8 mm yr^{-1} and 2.4 mm yr^{-1} for coral and no coral sites, respectively.

1.5 BIOTIC INTERACTIONS

The majority of CWC species are considered to be ecosystem engineers (Jones et al., 1994) because they induce long-term changes in the physical environment creating structural habitat that can be exploited by other organisms (Buhl-Mortensen et al., 2010). Reef-building species, when creating aragonite frameworks provide suitable hard

substrate for settlement by sessile fauna (Mortensen et al., 1995; Henry, 2001; Metaxas and Davis, 2005), as well as natural refuges for fish (Husebø et al., 2002; Costello et al., 2005; Harter et al., 2009) and other mobile species. A well-known symbiotic relationship exists between the scleractinian *L. pertusa* and the polychaete *Eunice norvegica* (Wilson, 1979a; Winsnes, 1989; Jensen and Frederiksen, 1992). The worm inhabits the coral framework building parchment-like tubes that are subsequently calcified by the coral. It feeds on food particles trapped in the host's polyps acting as a facultative kleptoparasite, but it also cleans and provides protection from potential predators indicating a mutualistic benefit (Mortensen, 2001). Moreover, this polychaete enhances coral calcification and anastomosis (Roberts et al., 2005) without disturbing the metabolic activity of its host (Mueller et al., 2013) and, thus, highly contributes to the growth and functioning of the reef ecosystem.

Coral gardens also offer a number of microhabitats for associated species (Miller et al., 2012; Appendix E: de Matos et al., 2014a). In the northern Gulf of Mexico, gorgonians *Callogorgia* occur in great densities between depths of 200 and 1000 m and are often found with egg cases of scyliorhinid catsharks (Etnoyer and Warrenchuk, 2007). Several host-specific associations have been described such as the shrimp *Bathypalaemonella serratipalma* on gorgonians *Iridogorgia splendens* (Watling, 2010) or the galatheid *Uroptychus* inhabiting only the antipatharian *Parantipathes* sp. (Cho and Shank, 2010). An example of high host fidelity is displayed by the brittle star *Ophiocreas oedipus* and the gorgonian *M. melanotrichos*, where no other symbionts seem to be allowed to live on this coral host (Mosher and Watling, 2009). The species is always found firmly attached to the central axial stem of the colony.

The complex morphologies exhibited by CWCs enhance habitat heterogeneity promoting higher biodiversity, not only when these organisms are alive, but also after their demise, i.e. traces or skeletal remains (Henry and Roberts, 2007; Bongiorno et al., 2010; Buhl-Mortensen et al., 2010). Along the Norwegian shelf margin, fish abundances were often higher in areas with biogenic substrate (coral rubble and coral framework) than in areas with substrates non-dependent of the reef expansion, such as hardground or soft sediments (Purser et al., 2013). Love et al. (2007) found over 2500 invertebrate specimens on a dead colony of the antipatharian *Antipathes dendrochristos* collected off southern California, on which sea anemones, brittle stars, crinoids and corophioid amphipods were the most representative groups. The nature of CWC interactions with associated fauna is, however, not straight forward and in many cases is still not well

understood (Auster, 2005). Buhl-Mortensen and Mortensen (2004a: Table 1) accounted for 983 invertebrate species living in close association with 74 corals, and of these, most are facultative symbionts. Also, functional connections between CWC habitats and fisheries resources have long been assumed (Costello et al., 2005; Ross and Quatrini, 2007), but evidence that those habitats were essential for the survival of associated species was only recently detected. For instance, high prevalence of the redfish larvae (*Sebastes* sp.) were found trapped on the tissues of various species of pennatulaceans, mainly *Anthoptilum grandiflorum* and *Pennatula aculeata* (Baillon et al., 2012).

1.6 THREATS AND CONSERVATION MEASURES

Cold-water coral ecosystems are globally threatened by an increasing number of anthropogenic activities, particularly on the high seas (Benn et al., 2010). Of these, the most widely known is deep-sea fishing, in particular bottom trawling (e.g., FAO, 2009; Auster et al., 2011). Trawling gear has been compared to forest clear-cutting practices due to its detrimental mode of operation, whereby heavy metal equipment is dragged along the seabed at high speeds (Watling and Norse, 1998). The discovery of substantial fish aggregations on seamounts and other topographic seabed features during the 1970's resulted in intensive and widespread fishing at those locations (Clark et al., 2010). Representative deep-sea fishes found to take advantage of those oceanographic features include the alfonsino (*Beryx splendens*), orange roughy (*Hoplostethus atlanticus*), black cardinalfish (*Epigonus telescopus*), toothfish (*Dissostichus eleginoides*), and roundnose grenadier (*Coryphaenoides rupestris*) among many others (e.g., Uchida and Tagami, 1986; Koslow, 1996; Clark et al., 2007).

Trawl-induced disturbances have long-term effects on benthic biota that is usually composed of long-lived species with low fecundity (Kaiser et al., 2006; Davies et al., 2007). Consequently, extensive areas of bare seabed have been revealed in the heavily trawled seamounts of the southwest Pacific (Koslow et al., 2001; Clark and O'Driscoll, 2003; Clark and Koslow, 2007) and the northwest Atlantic (Waller et al., 2007). Quantitative repeated surveys on seamounts off Tasmania have shown that *S. variabilis* thickets (a dominant scleractinian species in unfished areas) were almost absent from trawled grounds, with no evidence of clear recovery or re-growth five years after trawling ceased (Althaus et al., 2009). Similarly, minor signs of recovery were observed in seamount coral assemblages of New Zealand five years after the end of

trawling events (Williams et al., 2010). Both studies, however, noticed the presence of chrysogorgiid gorgonians, but it could not be determined if these were indeed new recruits or only vestigial fishing survivors of earlier fishing. Loss of habitat integrity has also been widely described for the coral mounds of the northeast Atlantic (Grehan et al., 2005; Wheeler et al., 2005). Instead of coral framework, Hall-Spencer et al. (2002) frequently found patches of living colonies of *L. pertusa*, often broken or detached from the seabed in trawled grounds off western Norway.

As a non-selective gear, considerable amounts of non-target invertebrate species have been incidentally captured by trawling, with CWC standing out in high proportions (Probert et al., 1997). Over three hundred tonnes of corals and sponges were harvested as bycatch in British Columbia's trawl fishery during the period from 1996 to 2004 (Ardron et al., 2007). Trawl catches from the orange roughy fishery on the South Tasman Rise showed, again, high levels of bycatch, among which *S. variabilis* was predominant (Anderson and Clark, 2003). Moreover, in a large area comprising the Flemish Cap, Flemish Pass, and Grand Banks of Newfoundland, corals were recorded in 69 % of the tows from groundfish bottom-trawl surveys (Murillo et al., 2011), indicating average captures of 3 species per tow (maximum number observed = 14).

Other severe impacts that cannot be overlooked in trawled grounds relate to physical changes in the submarine landscape due to displacement, re-suspension and removal of seabed sediments (Puig et al., 2011). Here, it is shown that the morphologic complexity of the seabed is being drastically reduced by trawl operations over large spatial scales on the northern Catalan margin (northwestern Mediterranean). Altering suitable settlement substrate (e.g., boulders, cobbles, gravel, sand, mud) can modify community composition having direct implications on ecosystem functioning (Levin et al., 2010).

Static gears such as bottom longline also represent a widespread threat to CWC ecosystems (e.g., Parker and Bowden, 2010; Durán Muñoz et al., 2011). These are often used in areas of complex topography due to the greater difficulty trawlers have in accessing those types of habitats (i.e. hard substrates that are generally coral-suitable habitats). Observer's data from commercial fisheries in Alaska shows that corals and sponges are frequently caught during longline or trap fishing, albeit at rates four times lower than by bottom trawling activities (Shester and Ayers, 2005: Fig. 1). In spite of this, underwater observations of longline operations indicate direct physical disturbance by the main line in many sessile species during the hauling process, some of which

although injured were never brought to surface (Welsford and Kilpatrick, 2008). The authors estimated that the area of seabed impacted by longlines was comparable with the areas swept by bottom trawls.

In light of the development of more efficient gears and advanced sonar technologies, actions to assess the environmental impacts of large-scale demersal fisheries, to identify VMEs, and to improve marine protected areas, have been the focus of a number of calls and initiatives from the United Nations during the last decade (e.g., UNGA, 2007, 2009). For the Azores, a number of spatial designations and management measures seeking sustainable fishing practices and the conservation of marine habitats have long been implemented by decision makers at the Regional Government. For instance, the *Dollabarat reef* and *Formigas islets* were designated as a Nature Reserve in 1988 and an OSPAR Marine Protected Area (MPA) in 2006 (see also DLR 47/2008/A of 7 November). Although temporary, Condor de Terra Seamount, located to southwest of Faial Island, is an example of a fishery closure in the region (Morato et al., 2010; PT Regional decrees 48/2010, 47/2012 and 88/2014). Both areas harbour rich, sessile, benthic assemblages comprising many CWC species (Braga-Henriques et al., 2006; OSPAR, 2010a; Appendix E: Tempera et al., 2012b). Driven by the global call for the conservation of benthic habitats from bottom fisheries, bottom trawling has been banned within the Azores exclusive economic zone (EEZ) since 2005 (Council Regulation (EC) No. 1568/2005; see Probert et al., 2007). Nevertheless, it should be noted that until 2003 the waters around the Azores were fully closed to trawl fisheries through regional legislation. Additionally, Portugal is a signatory to the CITES, the intergovernmental treaty that aims to restrict international trade of protected species including some coral groups. Although illegal trade of this kind can generate great amounts of money such as in the jewellery industry of *C. rubrum* (see Tsounis et al., 2010), to my knowledge, there is no harvesting of precious corals for trade purposes in the Azores.

Table 1.2 Age and growth rate estimates for a variety of cold-water coral species. Asterisks indicate species with known distribution in the Azores (see Chapter 2, Table 2.4). Codes: Time-series measurements – TS-M; Growth rings – GR; Amino acid racemization – AaR.

Species	Growth radial (mm y ⁻¹)	Growth axial/ vertical (cm y ⁻¹)	Age (years)	Method	Location	Depth (m)	Reference
Alcyonacea (gorgonians)							
<i>Acanella arbuscula</i> *	>0.020	>0.30	<100	Bomb ¹⁴ C	NW Atlantic ¹	526	Sherwood and Edinger (2009)
	0.070	1.00	30	GR			
<i>Corallium niobe</i> *	0.11±0.02	n/a	180±40	Excess ²¹⁰ Pb	Florida straits	600	Druffel et al. (1990)
<i>Corallium secundum</i>	0.170	n/a	67±9–71±9	Bomb ¹⁴ C	Hawaii	450±40	Roark et al. (2006)
<i>Corallium</i> sp.	n/a	0.43	67–>200	²¹⁰ Pb	Davidson Seamount	1482	Andrews et al. (2005)
<i>Isidella tentaculum</i>	0.084–0.12	1.14–1.67	53±10	²¹⁰ Pb	Gulf of Alaska	874	Andrews et al. (2009)
<i>Keratoisis ornata</i>	0.074±0.006	0.93±0.08	94±7	Bomb ¹⁴ C	NW Atlantic ¹	601	Sherwood and Edinger (2009)
<i>K. ornata</i>	0.075±0.011	n/a	200±30	¹⁴ C	NW Atlantic ¹	1193	Sherwood and Edinger (2009)
<i>K. ornata</i>	0.053±0.009	n/a	138±23	²¹⁰ Pb	NW Atlantic ¹	713	Sherwood and Edinger (2009)
<i>Keratoisis</i> sp.	0.051–0.057		89–282	²¹⁰ Pb	Davidson Seamount	1425, 1574	Andrews et al. (2009)
<i>Keratoisis</i> sp.	0.05–0.2			GR	Off New Zealand	935	Tracey et al. (2007)
<i>Keratoisis</i> sp.	0.05	0.19–0.44	131	²¹⁰ Pb/ ²²⁶ Ra		1425	Andrews et al. (2005)
<i>Keratoisis</i> sp.	0.05	n/a	~400	²¹⁰ Pb	SE of Tasmania	~1000	Thresher et al. (2004)
	0.1			EpMA ²			Thresher et al. (2007) ²
<i>Lepidisis</i> sp.	0.13–0.29	n/a	26–61	²²⁶ Ra/ ²¹⁰ Pb	Off New Zealand	690–800	Tracey et al. (2007)
<i>Paragorgia arborea</i>	0.830±0.120	0.162±0.022	80±11	Bomb ¹⁴ C	NW Atlantic ¹	414	Sherwood and Edinger (2009)
<i>Paramuricea</i> spp.	0.092±0.018, 0.205±0.020	0.56±0.05, 0.58±0.08	71±6, 103±14	Bomb ¹⁴ C	NW Atlantic ¹	814, 850	Sherwood and Edinger (2009)
<i>Primnoa resedaeformis</i>	0.36	0.16–0.232	>100	²¹⁰ Pb	SE of Alaska	263	Andrews et al. (2002)
<i>P. resedaeformis</i>	0.044	0.15–0.250	210–>300	¹⁴ C	NE Channel	450	Risk et al. (2002)
<i>P. resedaeformis</i>	0.090±0.008– 0.215±0.037	1.00±0.09– 2.61±0.45	23±4–100±9	GR	NW Atlantic ¹	414	Sherwood and Edinger (2009)

Table 1.2 (continued)

Species	Growth radial (mm y ⁻¹)	Growth axial/ vertical (cm y ⁻¹)	Age (years)	Method	Location	Depth (m)	Reference
Antipatharia (black corals)							
<i>Antipathes dendrochristos</i>	0.121	1.5	140±5	GR, ²¹⁰ Pb, ¹⁴ C	Off S California	106	Love et al. (2007)
<i>Antipathes dichotoma</i>	0.130–1.14	n/a	12–109	Bomb ¹⁴ C	Hawaii	50±5	Roark et al. (2006)
<i>Leiopathes</i> cf. <i>glaberrima</i> *	≤0.01	n/a	2377±15	Bomb ¹⁴ C	Hawaii	450±40	Roark et al. (2006)
<i>Leiopathes</i> cf. <i>glaberrima</i> *	0.014–0.015	n/a	198–483	GR, ²¹⁰ Pb	SE of USA	307–697	Williams et al. (2006, 2007)
<i>Leiopathes</i> sp.	0.005–0.013	n/a	350–4250	¹⁴ C	Hawaii	400–500	Williams et al. (2010)
<i>Leiopathes</i> sp.	0.008–0.022	n/a	530–2100	¹⁴ C	SE of USA	304–317	Prouty et al. (2011)
<i>Leiopathes</i> spp.*	5–3	n/a	275–2320	¹⁴ C	Azores		Carreiro-Silva et al. (2013) ³
<i>Stauropathes arctica</i>	0.033±0.011– 0.066±0.011	1.22±0.46– 1.36±0.20	55±8–82±31	Bomb ¹⁴ C	NW Atlantic ¹	876, 812	Sherwood and Edinger (2009)
Scleractinia (stony corals)							
<i>Desmophyllum dianthus</i> *		0.05–0.20	>200	²²⁶ Ra/ ²¹⁰ Pb	S of New Zealand	395, 335, 722	Adkins et al. (2004)
<i>Enallopsammia rostrata</i> *	~0.07 (at base)	~0.05	>100	²²⁶ Ra/ ²¹⁰ Pb	N Atlantic		Adkins et al. (2004)
<i>Madrepora oculata</i>	n/a	0.3–1.8 (5 polyps)	n/a	TS-M	NW Mediterranean		Orejas et al. (2008)
<i>Lophelia pertusa</i>	n/a	1.5–1.7 (4 polyps)	n/a	TS-M	NW Mediterranean		Orejas et al. (2008)
<i>L. pertusa</i>							Brooke and Young (2009)
Zoantharia (zoanthids)							
<i>Gerardia</i> sp.	~0.005	n/a	1800±300 (basal)	¹⁴ C	Florida Straits	610–630	Druffel et al. 1995
<i>Gerardia</i> sp.	n/a	n/a	250±70	AaR	Off Bahamas	630	Goodfriend (1997)
<i>Gerardia</i> sp. (fossil)	0.014–0.045	n/a	450±30–2742±15	Bomb ¹⁴ C	Hawaii	450±40	Roark et al. (2006)
<i>Gerardia</i> sp. (live-collected)	0.015	n/a	807±30	Bomb ¹⁴ C	Hawaii	450±40	Roark et al. (2006)

¹Off Newfoundland and Labrador;²Corrected value using EPMMA analysis (electron probe microanalysis).³For details see Appendix E - Joint publications produced as Ph.D. candidate relevant to this thesis.

Besides fisheries, other services provided by the deep sea merit growing concern and are currently high priority issues on the international political and research agendas (Barbier et al., 2014). Those encompass seabed mining (Sharma, 2007; Hein et al., 2009; Schlacher et al., 2013), hydrocarbon exploration (Glover and Smith 2003; Thurber et al., 2014), and also bioprospecting for natural products (Skropeta, 2008; Thornburg et al., 2010). The deep sea constitutes an exceptionally promising resource for carbon dioxide sequestration and exploitation of mineral deposits such as manganese nodules, cobalt-rich ferromanganese crusts (Hein et al., 2000) and polymetallic sulphides (Pandey, 2013). For example, deep-sea mud in the Pacific Ocean contains high concentrations of rare earth elements and yttrium, both essential in emerging technologies (Kato et al., 2011). Nevertheless, the scientific community and International Seabed Authority draws attention to the importance of conducting environmental impact assessments (ISA, 2008) before moving into an era of intense deep-sea exploration and exploitation (see Hein et al., 2013: Fig. 10). Recent studies argued that the impacts of deep-sea mining would be greater than trawling and even proposed the implementation of buffer zones between mining locations and protected areas (Boschen et al., 2013; Schlacher et al., 2013). Researchers also consider the creation of deep-sea reserves to be a crucial measure to restore impacted areas and protect deep oceans from increasing commercial activities (Barbier et al., 2014). However, the potential effectiveness of restoration measures in CWC ecosystems is uncertain.

1.7 RATIONALE, AIMS AND STRUCTURE OF THESIS

This thesis seeks to contribute to a better understanding of the poorly known cold-water coral ecosystems in a large and topographically complex area such as the Azores EEZ (≈ 1 million km²) and, thus, provide advice on ecosystem-based management policies.

In Chapter 2, I review pulses of coral collection in the Azores EEZ since the mid-Nineteenth Century, revealing the importance of those historical surveys for the current taxonomic knowledge. In addition, historical scientific observations and long-term fisheries bycatch are combined to assemble CWC occurrences as a faster and less-expensive assessment approach due to the paucity of presence data from visual surveys. A wide-area data set have been then produced. Here, CWC hotspots are identified and mapped within the 200-mile limit of the EEZ, providing valuable insights into the design robust strategies for ecosystem-based ocean and fisheries management. I also

present a detailed taxonomic inventory of the regional coral fauna with over 160 valid species listed (most from georeferenced data). Potential endemism and zoogeographic affinities of the Azorean fauna is discussed and correlated with aspects of species dispersal ability. Furthermore, spatial trends in CWC assemblage composition are investigated according to three factors: (1) feature type (island or seamount), (2) longitudinal section of the EEZ and (3) depth interval.

In Chapter 3 ROV transect data is used to examine the local-scale distribution of CWC assemblages in Condor de Terra Seamount (northeast Atlantic). This chapter presents baseline ecological data for poorly-studied and vulnerable deep-sea habitats occurring in a traditional fishing ground, addressing information gaps that are necessary to tackle in support of seamount management approaches and future research.

Chapter 4 comprehensively investigates associated invertebrate life on CWC ecosystems. Section 4.1 describes direct observations of the deep-sea crab *Paromola cuvieri* (family Homolidae) in coral gardens and deep-sea sponge aggregations, and reinforces the putative value of those ecosystems as biodiversity hotspots, habitat providers and a source of living resources. I use a long-term deep-sea video archive of manned submersible dives coupled with recent ROV surveys to better characterize the carrying behaviour in this large-sized species. Such behaviour has been widely recognized as insufficiently documented and lacking high-resolution imagery and this work gathered a considerable amount of novel *in situ* information. Furthermore, megabenthic assemblages of sessile fauna where *P. cuvieri* occurred are described by means of video analysis methodologies in order to investigate the importance of the surrounding habitat in the selection of carried objects. Insights into the function of carrying behaviour are also provided.

The last section of chapter 4 (section 4.2) addresses the symbiotic association between pediculariid gastropods and their stylasterid hosts. Stylasterids are important components of coral gardens but ecological studies focusing on this group are scarce as well as epibiotic faunal observations. Therefore, I use a species frequently recorded in the upper bathyal depths of Azorean seamounts to identify hosted snails, to species-level, and determine the nature of this symbiotic relationship. A detailed description of *Pedicularia sicula* is provided based on shell morphological data at different growth stages (e.g. embryonic and trivalve stages) with particular emphasis on the protoconch-specific characters. By providing taxonomic and ecological data on poorly known associated fauna, this work seeks to elucidate how vulnerable these are to human-induced

disturbances, resulting in reduced coral abundances and habitat integrity loss due to their life history characteristics.

Chapter 5 provides an overview of the research undertaken during this thesis discussing main findings and how these have contributed to what is known about CWCs. The implications of these results for conservation initiatives balanced with sustainable fisheries are also discussed. This chapter concludes with suggestions for future work.

1.8 PUBLISHED PAPERS

The following manuscripts, which include the majority of the results presented in this thesis, have been published (3) or will be submitted to (1) international peer-reviewed journals:

- **Chapter 2**

Braga-Henriques, A., Porteiro, F. M., Ribeiro, P. A., de Matos, V., Sampaio, I., Ocaña, O., and Santos, R. S.: Diversity, distribution and spatial structure of the cold-water coral fauna of the Azores (NE Atlantic), *Biogeosciences*, 10, 4009–4036, doi:10.5194/bgd-10-529-2013, 2013.

- **Chapter 3**

Braga-Henriques, A., et al.: Observations of coral assemblages on a traditional fishing ground, Condor de Terra Seamount (NE Atlantic). DSR-II, to be submitted in 2015.

- **Chapter 4**

Section 4.1

Braga-Henriques, A., Carreiro-Silva, M., Tempera, F., Porteiro, F. M., Jakobsen, K., Jakobsen, J., Albuquerque, M., and Santos, R. S.: Carrying behavior in the deep-sea crab *Paromola cuvieri* (Northeast Atlantic), *Marine Biodiversity*, 42, 37–46, doi: 10.1007/s12526-011-0090-3, 2012.

Section 4.2

Braga-Henriques, A., Carreiro-Silva, M., Porteiro, F., Matos, V., Sampaio, Í., Ocaña, O., and Ávila, S. P.: The association between a deep-sea gastropod *Pedicularia sicula* (Caenogastropoda: Pediculariidae) and its coral host *Errina dabneyi* (Hydrozoa: Stylasteridae) in the Azores, *ICES Journal of Marine Science*, 68, 399–407, doi: 10.1093/icesjms/fsq066, 2011.