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Cold Temperate Coral Habitats

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Abstract

Cold-water coral habitats are constituted by a great variety of anthozoan taxa, with reefs and gardens being homes for numerous invertebrates and fish species. In the cold temperate North Atlantic, some coral habitats such as *Lophelia pertusa* reefs, and *Primnoa/Paragorgia* dominated coral gardens occur on both sides of the Atlantic over a wide latitudinal range. Other habitats, as some dominated by species of Isididae and Chrysogorgidae seem to have a more local/regional distribution. In this chapter, we describe the habitat characteristics of cold-water coral reefs, soft and hard-bottom coral gardens, and sea pen meadows with their rich associated fauna illustrated with numerous photos.

Keywords: cold-water corals, associated fauna, coral garden, coral reef, Scleractinia, Alcyonacea, gorgonians, Antipatharia

1. Main subtitles of chapter

- Cold water coral reefs; Lophelia
- Hard-bottom coral gardens:

Sections cover different communities with key coral species (e.g., Alcyonacea (Gorgonians), Antipatharia) and their associated fauna.

• Soft-bottom coral gardens:

Sections cover different communities with key coral species (e.g., Alcyonacea (Gorgonians), Antipatharia) and their associated fauna.

• Sea pen meadows:

Two sections covering shallow and deep water meadows and their associated fauna.



2. Introduction

"Coral reefs," "Coral gardens" (reef-forming Scleractinian corals and aggregations of gorgonians, black corals, and sea pens) and "sea pen and burrowing megafauna communities" are habitats classified by the Oslo Paris Convention for the Protection of the Marine Environment of the Northeast Atlantic (OSPAR) as "Threatened and/or declining" [1]. Sea pen and burrowing megafauna communities are also of key conservation importance as defined under Annex V of the 1992 OSPAR Convention [2, 3]. Coral gardens are sensitive to physical disturbance impacts caused by bottom trawling and activities related to the petroleum industry [4–6]. Bottom trawling is known to be one of the most destructive ways of fishing and causes reductions in habitat complexity, changes in species composition, and reductions in biodiversity [7–9]. These threats highlight that it is crucial to assess the ecological importance of these deepwater communities, to develop sound scientific advice for management of cold-water ecosystems [10, 11].

Corals include species from various taxonomic groups (including Scleractinia, Zoanthidea, Antipatharia, Gorgonians, Pennatulacea, and Stylasteridae). According to Roberts et al. [12], 65% of a total of 5160 coral species occur deeper than 50 m. Several of the groups (Gold corals, Antipatharia, Octocorallia, and Stylasterida) are represented by more species in deepwater than shallow.

Studies on cold-water corals have expanded dramatically in recent years and their role as habitat providers for a rich fauna has been shown in several studies [11–18].

Cold-water corals are found around the world, most commonly in the depth range of 200–1500 m [19–33]. Shallower, upper depth limits (up to 40 m) are found in Norway, New Zealand, Chile, and British Columbia and demonstrate that it is not the depth per se, but the vertical range of intermediate and deep water masses that controls the bathymetric distribution of these corals.

Corals typically create habitats elevated above the surrounding seabed (up to several meters) and occur on bottoms with mixed substrata in areas with relatively strong currents (**Table 1**). They offer a variety of microhabitats with different current speeds, food sources, and substrates. Most corals have an arborescent morphology with branches reaching out of the near-bottom boundary into the faster flowing water above. Corals have a complex 3-D architecture and provide substrata of different ages, due to their continuous growth and decay. Sheltered cavities within a colony often contain organic-rich sediments, while the outer parts provide a high water flow with elevated rates of food supply and little sedimentation.

The relative abundance of food at the shelf-slope transition argues against food limitation in this zone and focuses attention upon physical factors [34] to understand the distribution of cold-water corals.

Internal waves on continental margins can induce resuspension and even an upward transport of particles in periods of strong wind [35]. Here, biological structures such as corals can provide shelter and protection for some organisms against strong currents and predators and, at the same time, offer a reliable supply of detrital food within their interstices. Higher structures that reach into laminar currents above the more turbulent near-bottom currents may provide other food sources (e.g., zooplankton) [15].

Coral habitats	Habitat provision	Main key species	Associated fauna	Longevity of key species (years)
Cold-water coral reefs	Hard substrate, shelter, Elevated feeding position	Lophelia pertusa, Oculina varicosa, Madrepora oculata, Solenosmilia variabilis, Gonicorella dumosa, Enallopsammia profunda	Mobile: Fish, crustaceans, brittle stars, polychaetes. Sessile: Actiniarians, gorgonians, sponges, bryozoans, polychaetes	>1000
Hard-bottom coral garden	Shelter, elevated feeding position	Paragorgia arborea, Primnoa spp., Paramuricea spp., Callogorgia verticillata, Antipathes spp., Bathypathes spp., Leiopathes spp.	Mobile: Fish, crustaceans, brittle stars. Sessile: Actiniarians, parasitic crustaceans, polychaetes	50–300
Soft-bottom coral garden	Elevated feeding position, Shelter	Acanella arbuscula, Isidella lofotensis, Radicipes gracilis	Mobile: Crustaceans, polychaetes	50–100
Sea pen meadow	Elevated feeding position, shelter	Funiculina quadrangularis, Kophobelemnon steølliferum, Virgularia mirabilis, Pennatula phosforea, Halipteris spp., Umbellula encrinus	Sessile: Crustaceans, brittle stars	15–80

Table 1. Coral habitats.

In many ways, the biological habitat structures provide more food particles and other vital resources compared to the framing habitat. Often propagules and larvae are present in the deep-sea demersal plankton, but suitable firm substratum is lacking. Thus, organisms that provide an elevated position on a stable substratum represent a scarce habitat, contributing substantially to the species richness of their respective environments [15, 36].

It is known that coral habitats house a large assemblage of crustaceans, mollusks, ophiuroids, sponges, and fish [11, 15, 16, 37–42]. These organisms can use corals as a substrate for attachment and shelter [43], for feeding [44, 45] and parasitism [16]. The mobile fauna is particularly difficult to document [11, 15, 17, 41], but with the recent development of underwater video equipment, it has become possible to inspect coral colonies for even rather small associated organisms.

3. Cold-water coral reefs Lophelia pertusa

L. pertusa is common along the European margin and develops reefs in several places where the environmental conditions are right. The Northeast Atlantic can be divided into three main reef provinces based on geography and environmental similarities: (1) The Nordic occurrences, including Sweden, Norway, Faroe Island, and Iceland, (2) Irish-British margins, and (3) Franco-Iberian margin [46]. L. pertusa is also found along the mid-Atlantic ridge, but living reefs have not been confirmed and live coral is only represented by small scattered colonies [47]. However, large patches of coral rubble indicate proliferation of reefs occurred in the past. Changing ocean currents resulting from the

disappearing glaciers during the last deglaciation probably changed the environmental settings in a negative way for the coral.

On the North American margin, reefs are much less common than at the other side of the Atlantic. Larger reef structures in the eastern USA are only found from North Carolina and southward, and into the Mexican Gulf. The reason for this is not clear, but temperature variation caused by North Atlantic Drift, better known as the Gulf Stream, may prevent long-term stable conditions for reefs to develop in the northeastern USA-Canadian margin. A single reef occurrence in the mouth of the Laurentian Channel in Atlantic Canada is an exception to this [48]. This reef occurs in the southward flowing warm water that has passed the southern coast of Greenland after branching off the Gulf Stream south of Iceland. The recently discovered reef off southwest Greenland [49] occurs in the same water.

3.1. Environment

L. pertusa can use all kinds of hard substrate as a foundation, even human-made structures such as legs of oil platforms in the North Sea. In Norwegian waters, *Lophelia* reefs are found on finer sediments mixed with gravel as well as directly on bedrock. Occurrences on bedrock are found in fjords and coastal areas. Further from the coast, on the continental shelf and slope, bedrock is rare and morainic material with gravel and boulder on banks and edges of troughs is the most common reef foundation substrate [50]. Strong tidal currents, together with seasonal changes in temperature and wave energy, influence the habitats and generate large sand waves [51]. In these settings, the large biogenic structures formed by the reef-building *Lophelia* are found in the upper range [28, 32, 52, 53].

3.2. Morphology

At a local scale, the morphology of organisms shapes the environment by modifying the hydrodynamics and providing shelter, pockets with trapped particles, and other microhabitats. A coral reef can be defined as an aggregation of coral skeletons completely covering the substrate underneath (**Figure 1**). Colonial scleractinians need hard substrate for settlement. This substrate can be a shell or a pebble, and as soon as one colony is present, it provides a new hard substrate for subsequent colonization. Coral colonies may grow at one site for hundreds of years. During that time, it transforms the seabed to a complete cover of coral skeleton fragments through alternating growth, death, and fragmentation. When the bottom beneath the colonies consists of a layer of dead skeleton, the area can be termed a "coral reef." Corals growing on a steep surface may not develop reefs, but are rather called coral gardens. When the coral grows large, and break up, due to their own weight, skeletal fragments will not accumulate at the site but fall deeper, outside the favorable environment.

Cold-water coral reefs typically have a circular or elongated outline with a maximum length of c. 1000 m. At the Norwegian continental shelf, it is estimated that there are around 6000 *Lophelia* reefs [52]. Many of these reefs are several 100 m long and occur in clusters (reef complexes) up to 35 km long (Røst reef) [54]. Their area, however, covers less than 0.1% of the total

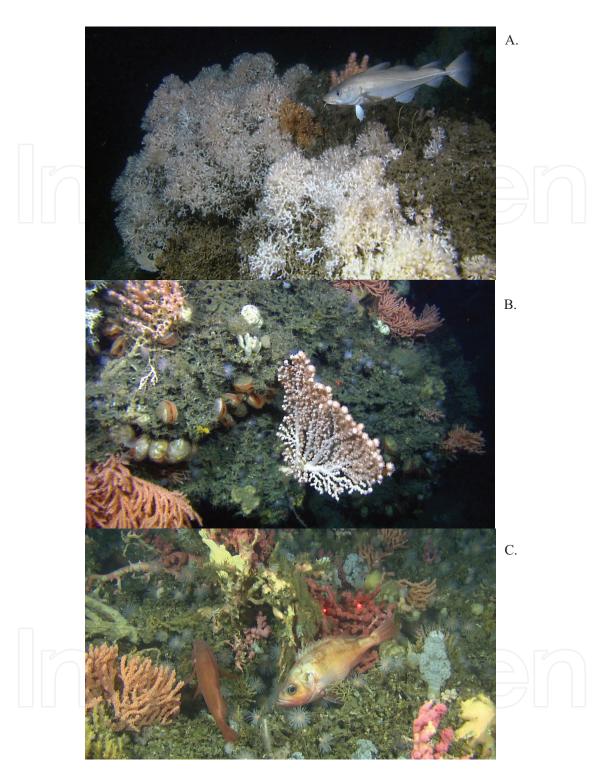


Figure 1. The cold-water coral reef habitat. (A) Summit of cold-water coral reef. Live Lophelia pertusa (white branches) together with a cod. (B) Lower part of Lophelia reef. Typically dominated by dead Lophelia being a substrate for gorgonian corals and other associated organisms. (C) Richness of old parts of a Lophelia reef with gorgonians that are overgrown with hydroids and sponges. Two redfish are taking shelter below the old *Paragorgia*. Red laser dots indicates a scale of 10 cm.

area of the depth zone where they occur. The reefs commonly have vertical zones, with living coral at the top and skeletal fragments at increasing stages of decay toward the bottom of the reef [55]. The reefs may have different shapes depending on currents and seabed topography.

3.3. Provision of habitat

Reefs represent large and complex structures that significantly increase habitat heterogeneity. Framing habitats is varied and offers a wide range of substrates, but the complexity of these large structures represents an increased variety of microhabitats that elevate local species diversity [16, 17, 42, 56]. The associated organisms of cold-water coral reefs are comprised mainly of species that occur on other hard-bottom substrates, and their relationships with the coral are facultative.

Three successive habitat zones can be observed when crossing a reef, namely (1) the coral rubble zone, bordering the framing habitats, consists of small pieces of skeleton, followed by (2) the coral block zone dominated between the foot and the top of the reefs, with mixed coral substrates dominated by larger dead blocks, which lead to (3) the top of the reef where live colonies proliferate.

Within coral colonies of the live reef, four distinct microhabitats can be recognized, namely (i) live coral tissue, (ii) surfaces of dead corals often slightly covered with detritus, (iii) cavities inside coral skeletons, and (iv) open space between coral branches.

Most coral-associated species are facultative symbionts without a direct relationship with the living corals and can survive in similar microhabitats on bottoms without corals [56]. The endosymbionts (mainly copepods) are an exception to this. Rather than the presence of live coral, it is the hard substrate, and thus the diverse microhabitats provided by dead coral skeletons, that facilitates the high biodiversity associated with reef-forming, cold-water corals [56] (and references therein) [42].

3.4. Associated fauna

There is a great species diversity of animals found together with cold-water, reef-forming corals [32, 56–59]; however, there are no examples of associated species with an obligate relationship between dead coral skeletons. The highest diversity of associated species is found in the zone with dead coral block [56, 59]. Here, the skeletons are exposed and occur with a higher three-dimensional complexity than in the rubble zone surrounding the reefs.

The live tissue of cold-water scleractinians seems to prevent attachment of sessile epibiotic species. Even among the few species that are commonly found intimately associated with living coral polyps, there are few examples of obligate relationships [15] (Figure 2). However, many of these species are rarely found in other habitats. The polychaetes *Eunice norvegica* and *Harmothoe oculinarum* are two good examples: *E. norvegica* lives in a close relationship with *L. pertusa*. The coral embed the parchment-like tube of the polychaete in its skeleton. After some years of skeletal growth, the tube of *E. norvegica* may contain several openings, each one close to a polyp, where it can search for food spills [60]. *E. norvegica* spends time searching for food, cleaning the coral's surface for organic particles, and removing organisms invading its territory or over-growing the coral [59]. The strategically located tube openings allow easy access to food trapped by *L. pertusa*. The polynoid polychaete *H. oculinarum* is a commensal that can be found inside the tube of *E. norvegica*. The highest diversity of associated species is found in the zone with dead coral block [56, 59]. Here, the skeletons are exposed and occur with a higher three-dimensional complexity than in the rubble zone surrounding the reefs.

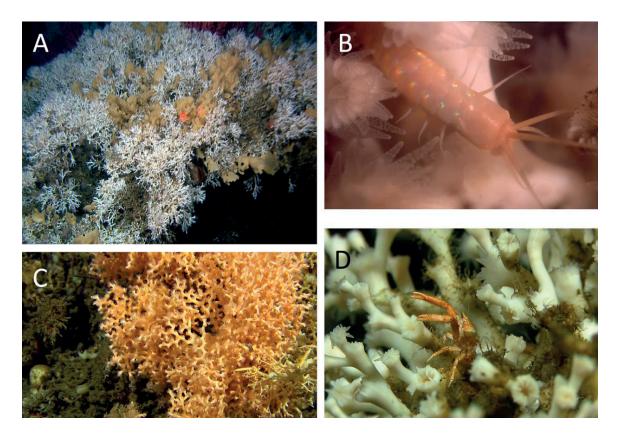


Figure 2. Close associates with Lophelia pertusa. A: Living part of a Lophelia reef with sponges. B: Eunice norvegica is a common polychaet living intimately with the polyps of Lophelia that rarely occur in other habitats. C: The scleractinian Madrepora oculata with the basket star Gorgonocephalus sp. (lower right). D: The squat lobster Munidopsis serricornis on the branches of Lophelia.

4. Hard-bottom coral gardens

4.1. Alcyonarian corals

The alcyonarian corals (soft corals) utilize a wide range of substrates, including semiconsolidated mudstone. Alcyonarian corals, in particular Nephtheidae, have a wide geographical and bathymetric distribution [33, 47]. The colonies are rather small (<30 cm) but may occur in relatively high densities (>500 colonies per 100 m²) [33]. The extent of patches of this coral group seems to be larger than for gorgonians. There are few known relationships documented with other invertebrates. The association between ophiuroids and nephtheids has been reported at various locations [61-63]. Mortensen [62] observed juveniles of the basket star, Gorgonocephalus eucnemis, parasitic on Eunephtia, and Fedotov [61] reports juveniles of Gorgonocephalus on colonies and within the polyps of *Drifa glomerata*. The foraminiferan *Planispirinoides bucculentus* has been observed on Duva florida off Nova Scotia [40]. Compared to the rigid structures of scleractinians and gorgonians, the soft coral represents an unstable substrate not suitable for attached species.

4.2. Gorgonian corals

Gorgonian corals provide habitats within and between colonies, when they occur in stands. The density of colonies within stands is typically higher for smaller species than for larger species [64]. This is illustrated by coral gardens off the Aleutian Islands (Alaska) [64–66] and Nova Scotia (Canada) [64], where smaller gorgonians and stylasteridae are found in densities of up to 200–400 colonies per 100 m². The larger gorgonian *Paragorgia arborea* occur less dense with a maximum of 49 colonies per 100 m². The gorgonian stands extend horizontally from 10 to 100 m [64]. In addition to accessing faster-flowing water above the bottom, colonies orient themselves toward the main current to maximize the amount of water passing the polyps [67]. The advantages of this morphologically enhanced feeding may also be utilized by suspension feeding and epizoic animal attached to the colony. In addition, the suspension feeders may also derive nutrition from detritus or microorganisms commonly found trapped in the mucus secreted by the gorgonians [13].

4.2.1. Associated fauna

The gorgonian-associated fauna is dominated by crustaceans, particularly amphipods. This is true for tropical gorgonians [68], which also host parasitic copepods, but deepwater gorgonian taxa exhibit a richer echinoderm fauna, including ophiuroids adapted to capturing particles in the elevated flows provided by the corals [39, 69]. The cold-water gorgonians have fewer decapods (crabs and shrimps) and gastropods than warm-water corals [13, 68]. In a study focusing on the associated fauna of cold-water gorgonians, Buhl-Mortensen and Mortensen [17] found that only a few specialized and obligate symbionts are connected to the live parts of corals. Among these are three highly specialized parasitic copepod species, presumably feeding on their hosts' coenenchyme [13]. The number of obligate symbionts is higher for gorgonians than for antipatharians, alcyonarians, and scleractinians. In their review of available literature, Buhl-Mortensen and Mortensen [17] reported 24 species having obligate relationships with 21 gorgonian host species. For comparison, only seven obligate symbionts have been reported for four scleractinians.

4.2.2. Habitat provision

Primnoa resedaeformis and *P. arborea* are the most abundant and widely distributed large gorgonians in the North Atlantic [25, 30, 33, 64, 70], where they can form stands or "coral gardens" (**Figure 3**). They are among the largest cold-water gorgonian corals, reaching a height of 50–250 cm. These corals offer two different microhabitats for associated species: (i) the clean and living surface of coral tissue in the younger parts of the colony and (ii) pockets of detritus and exposed skeleton in the older parts.

4.2.3. Associated fauna

P. arborea and *P. resedaeformis* host a rich fauna, dominated by suspension feeders using the coral as substratum or mobile animals using it as a refuge against predators [15–17] (**Figure 4**). The fauna composition differs for the two corals, but consists mainly of species also occurring in other habitats. However, a few highly specialized parasites have been identified associated with each of the species [15–17]. The abundance and species richness of the associates are significantly correlated with the host morphology, such as number of

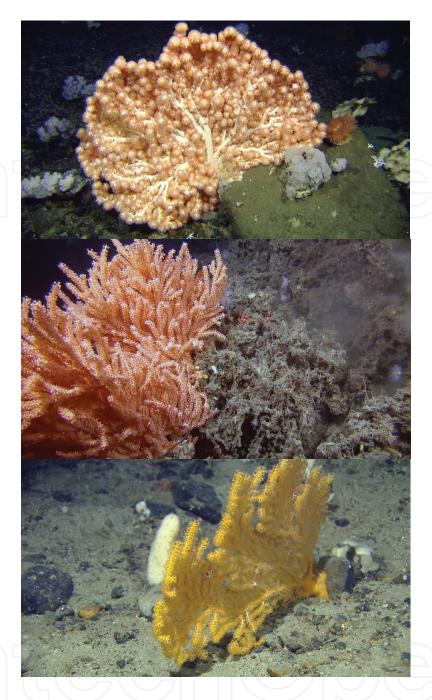


Figure 3. Hard-bottom coral gardens. Three species that form hard-bottom coral gardens are the "bubble gumme" coral Paragorgia arborea, on top, Primnoa resedaeformis, in the middle, and Paramuricea placomus. P. arborea can reach several meters in height and widths, while the two other species normally reaches a height of 20-70 cm.

branches and area of exposed skeleton. Even though the cold-water gorgonians support fewer obligate associations, several of the associated species are rare in other habitats and seem to prefer gorgonian species [15].

Close inspection of *P. arborea* using video [71] shows that crustaceans are the most common group of associates. Amphipods belonging to the family Stegocephalidae were found on 26% of the colonies, and other common crustacean associates were shrimps and hermit crabs.

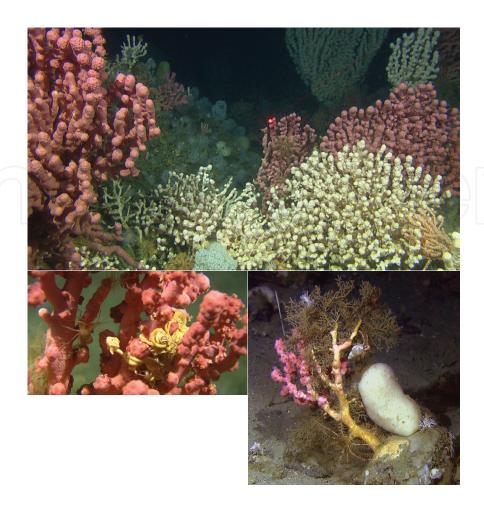


Figure 4. Habitats hard-bottom coral gardens. The larger sea trees can form forest-like habitats (upper photo). Here, we find a mixture of coral species. Shrimps are hiding between the branches, and the large "Basket star" Gorgonocephalus sp. is feeding from their elevated position on the branches of Paragorgia arborea. (photo lower left). It is the oldest parts of the colonies that hosts the riches associated fauna (photo lower right). Her we often find hydroids, crinoids and even hermit crabs. Bellow the old colony is a sponge.

Galls of the endoparasitic copepod Gorgonophilus canadensis, which is highly adapted to its host P. arborea [16], has been observed on both sides of the North Atlantic. In addition to parasitic copepods, the ophiuroid Gorgonocephalus is one of very few examples of host-specific associates. It uses the elevated position offered by P. arborea to collect particles (detritus or plankton) from the water passing by.

4.3. Antipatharia

North Atlantic black corals (Antipatharia) appear to be restricted to open ocean areas with Antipathes erinaceus, Distichopathes sp., Phanopathes sp., and Stauropathes punctata only recorded on Josephine seamount, the Azores, and Cape Verde Islands [72]. Around the Azores, Antipathella wollastoni is the most common species in deep infralittoral and circalittoral grounds (>20 m) and is known to form dense stands. In bathyal areas, the black corals, Leiopathes spp., are common between 200 and 600 m and can grow to a height of 2.5 m [73, 77].

4.3.1. Associated fauna

Black corals have many associated epifauna, most commonly serpulid worms, bryozoans, and ascidians, and the number of epibionts of Antipathella subpinnata shows an increase with the age of the corals and decrease with the depth [74].

5. Soft-bottom coral gardens

5.1. Gorgonian corals

Most gorgonians are confined to hard bottoms, except for some species of Isididae and Chrysogorgiidae, such as Isidella lofotensis, Acanella arbuscula, and Radicipes gracilis, which attach to sandy and muddy bottoms with root-like holdfasts (Figure 5).

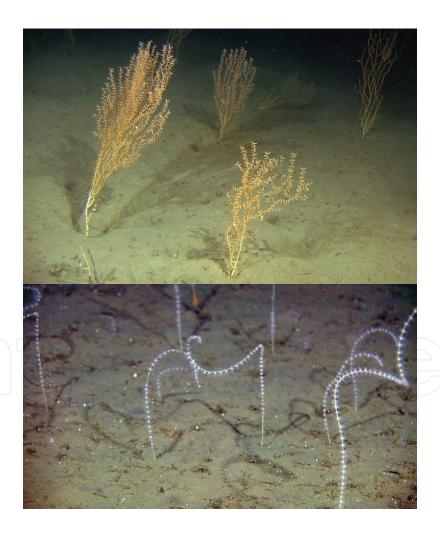


Figure 5. Soft-bottom coral gardens. The bamboo coral *I. lofotensis* is in the Norwegian Hardangerfjord and in the Norwegian through forming coral gardens at a depth of 200–300 m depth (upper photo). This species is only known from Norwegian waters. In deep and cold North Atlantic waters the gorgonian Radicipes "pigtail coral" forms coral gardens.

Soft-bottom bamboo coral gardens are found on both sides of the North Atlantic, represented by two species with different geographic ranges. The geographic barrier represented by the Greenland-Scotland Ridge separates the Nordic Seas and the North Atlantic. To the south of this, *A. arbuscula* occur sometimes with sea pens and the solitary scleractinian cup coral *Flabellum alabastrum* [33, 75], while on the other side of the barrier, in the North Sea and the Norwegian Sea, *I. lofotensis* occur in troughs and fjords [76]. In the western North Atlantic, *A. arbuscula* is found in the upper and middle bathyal (200–1000 m depth), while in the eastern North Atlantic, it occurs deeper (1800–2700 m depth) in the lower bathyal zone [69].

5.1.1. Associated fauna

In the western North Atlantic, the brittle *star Ophiomuseim lymani* is often found on *A. arbuscula* and assemblage. From the eastern side, Buhl-Mortensen and Mortensen [40] found that the polynoid polychaeta *Eunoe spinulosa* was strongly associated to this coral. Very little is known about the associated fauna of *Isidella* and *Radicipes*.

6. Sea pen medows

Sea pens are slender anthozoans reaching 0.1–2 m above the bottom accessing the elevated bottom currents. They provide predation shelter and good position for particle collection away from the slower current in the near-bottom boundary layer. Although the number of studies is limited, sea pens appear to have fewer associated organisms compared to scleractinians and gorgonians. *Funiculina quadrangularis* is a species with greatest conservation importance in the greater North Sea and Celtic Sea areas [78]. It can become a little more than 2 m tall, with approximately one quarter of the lower part of the structure embedded in the sediment [78]. Predators on sea pens include nudibranchs, which have been observed preying on sea pen polyps. The nudibranch *Armina loveni* is a specialized predator on the sea pen *Virgularia mirabilis*. It is infrequently recorded but known to occur from Norway to Western France. In Puget Sound (western USA), a related species, *Armina californica*, is one of the predators on *Ptilosarcus gurneyi* [79]. Many specimens of *V. mirabilis* lack the uppermost part of the colony, a feature that has been attributed to predation by fish.

6.1. Associated fauna

The associated fauna of sea pens is poor compared to gorgonian corals. In a study of >1000 sea pens from Norway [71], only 4% of the colonies had fauna on them, but 15% had organisms sitting near the colony. The squat lobster *Munida* sp. was found close to 8% of the 584 *Kophobelemnon stelliferum* colonies studied (**Figures 6** and 7). It appears to use the sea pen as a base station for scavenging, active hunting, and sheltering against predators. Sea pens



Figure 6. Sea pen meadows. *K. stelliferum*, upper photo, is together with *Pennatula phosphorea*, two common and relatively small sea pens (10–20 cm) forming "sea pen meadows" in the North Atlantic. There are few associates living on them, but organisms are often found to hide below a sea pen, likely as a protection against predators. Below *K. stelliferum*, we see two *Munida* squat lobsters and sitting on the *P. phosphorea* is a shrimp and an ophiuroid.

have stinging cells and often emits light that could scare away the potential predators of the organisms seeking shelter under these [80]. The only associated species found on *F. quadrangularis* was the ophiuroid *Asteronyx loveni* that has a close relationship with its host that is also reported from the west coast of Scotland [81]. The sea pen provides a suitable feeding platform in an elevated position for particle collection away from the slower current in the near-bottom boundary layer [39]. *A. loveni* catches small pelagic animals, mainly copepods, for food, but polyps and mucus of from sea pens have also been reported as stomach content [39]. It has been suggested by Buhl-Mortensen and Mortensen [40] that the relationship with the host could be mutualistic as, *A. loveni* could keep colonies clear of sediment and therefore, making them less vulnerable to smothering. Associated fauna has only in very few occasions been found on the sea pens *Pennatula phosphorea* and *V. mirabilis* [71].

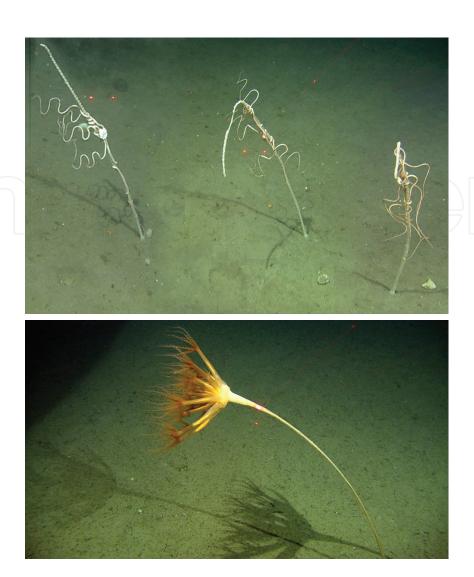


Figure 7. Sea pen meadows, Funiculina quadrangularis, upper photo, and Umbellula encrinus are among the largest sea pens (1-2.5 m) in the North Atlantic. They form sea pen meadows at larger depths and firmer substrate than the smaller sea pens. U. encrinus occur at 900 m in arctic waters off Norway. These large sea pens have few associated organisms, but there is a strong and likely mutualistic relation between the ophiuroid Asteronyx loveni and F. quadrangularis. In upper photo (a compilation of three photos), we see how the ophiuroid stretching outs its arms uses its elevated position to catch particles from the water.

7. Conclusion

Clearly, cold-water coral habitats in the North Atlantic represent several different ecosystems, with different species compositions and habitat characteristics. Coral garden is a heterogeneous habitat covering contrasting environments and a wide range of anthozoan taxa. A main division of this habitat relating to substrate (hard vs. soft seabed) is relevant to provide better consistency of habitat definitions. Further subdivisions are presented in this chapter. Main problem of management of cold-water coral habitats is still a lack of knowledge. Mapping of these habitats cannot rely only on bycatch records from the fishing fleet. Directed mapping of identified priority areas should be carried out before new industries move into deeper oceanic waters. Climate change (increased temperature, changing current patterns, and other indirect effects) represents a pressure that could compromise the coral livelihood differentially in different areas. There is a risk that the combined effect of human impact and climate change will cause greater negative effects in some places than anticipated today.

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