Trophic Ecology and Habitat Provision in Cold-Water Coral Ecosystems

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Contents

1 Introduction ................................................................................... 2
   1.1 Types of CWC Animal Forests .................................................... 3

2 Trophic Ecology ........................................................................ 5
   2.1 Framing Environment ............................................................... 5
   2.2 Food Transport by Near-Bottom Currents ................................. 5
   2.3 Feeding in Cold-Water Coral Forests ...................................... 7

3 Cold-Water Corals as Habitat Providers and Biodiversity Hot Spots .... 9
   3.1 Sea Pen Stands ........................................................................ 11
   3.2 Hard-Bottom Coral Gardens .................................................. 13

4 Cold-Water Coral Reefs .............................................................. 16
   4.1 Habitat 1: Live Coral Zone ..................................................... 17
   4.2 Habitat 2: Dead Coral Zone ................................................... 18
   4.3 Habitat 3: Rubble Zone .......................................................... 18

5 Cold-Water Coral Forests as Feeding Place and Nurseries for Fish ...... 19

6 The Role of Symbionts .................................................................. 20

7 Coral Associates in Cold Versus Warm Waters ................................ 21

8 Conclusion .................................................................................. 22

9 Cross-References ........................................................................ 23

References ..................................................................................... 23

Abstract

Cold-water coral ecosystems differ from each other greatly in structure, faunal makeup, and ecological function. Attributes such as substrate type, 3-D complexity, biological community, and nutrient supply also change over small temporal...
and spatial scales. In this chapter, we present an overview of food gathering strategies employed by a range of cold-water corals. Furthermore, the importance of corals as habitat providers for associated fauna and thus biodiversity is discussed. The coral habitats support ecosystems at various spatial scales ranging from local exposed skeleton patches on gorgonian branches to the various zones on a reef. Comparison is made between many types of animal forests made up by cold-water corals, including several types of coral gardens and coastal and offshore reefs from a wide range of environmental settings. The trophic ecology of reef types is compared, and the variation in feeding behavior across particular reefs is also discussed.

**Keywords**
Animal forest • Cold-water coral reef • Coral garden • Trophic ecology • Associated fauna • Filter feeders

1 **Introduction**

Cold-water corals (CWC) can form animal forests (see chapter “Animal Forests of the World: An Overview”) of great structural variety, in response to local environmental and food supply conditions, within a range of cold-water environments. CWC animal forests have previously been characterized as either “reefs” or “coral gardens” (OSPAR 2008a, b). More specific classification of these CWC forests has been predominantly determined by the composition of key taxa constituting the “forests.” Scleractinian corals, in both shallow and deep waters, may develop reefs with multigenerational growth on hard or mixed substrates (colonial- or pseudocolonial scleractinians) or occur in relative high densities as cup-coral fields on soft substrates (solitary scleractinians). The difference between colonial and pseudocolonial can be illustrated with the common species *Lophelia pertusa* and *Paragorgia arborea*. Polyps in a colonial species like *P. arborea* share internal organs and are connected with living tissue, while *L. pertusa* lack such connections. The individual polyps of *L. pertusa* are only connected with an outer mucoid coenenchym. Whether the cup-coral fields fall into a strict definition of coral garden (CG) or forest is unclear and illustrates the fact that the defining criteria are not well established. The diversity of habitats comprised by octocorals is much higher than for hexacorals, with representatives on both hard and soft substrates. Little is known about the CWC forests’ trophic support of associated species and other ecological functions of corals in deep-water ecosystems or how these may be linked with the shallower shelf and pelagic ecosystems.

In this chapter, we will present an overview of what is known about trophic ecology and ecosystem functioning for CWC forests. We will focus on provisioning functions and services related to trophic support, habitat provision, and biodiversity support.
1.1 Types of CWC Animal Forests

The ecosystem functioning support is a common attribute for CWC forests that could be used to explain why some anthozoan communities are regarded as “special and valuable” habitats (e.g., reefs and CG) whereas others (e.g., sea anemones) are regarded as “common” species. The operational definitions of the special anthozoan habitats are largely based on expert evaluation, and the confusion of terminology is clearly illustrated for the sea pens.

The division of classes of CWC forests used in this chapter is the following:

1. Sea pen stands (sea pen and burrowing megafauna communities)
2. Coral gardens, including:
   (a) Soft-bottom coral gardens
      (i) Cup-coral fields
      (ii) Scleractinian gardens
   (b) Hard-bottom coral gardens
3. Cold-water coral reefs

Sea pens may occur in dense stands (identified as “seapen and burrowing megafauna communities” by OSPAR (Curd 2010)) or may be important members of CG (Christiansen 2010), (OSPAR designates all gorgonian communities of a certain density of colonies as CG). CG can consist of very different species and groups of corals inhabiting the seafloor in close spatial proximity. It is therefore entirely appropriate to split this loosely defined biotope into “soft-bottom CG” and “hard-bottom CG.”. Most gorgonian corals live on hard bottom, but some species of Isididae and Chrysogorgiidae corals and Antipatharia (black corals) can form dense stands on sandy mud (e.g., Radicipes gracilis and Isidella lofotensis in Norwegian waters, and Acanella arbuscula in the western and central Atlantic). Isidella is mainly found at 300–400 m depth, in the larger fjords of Norway (Hardangerfjord, Trondheimsfjord, and Andfjord) (Buhl-Mortensen and Buhl-Mortensen 2013) (Fig. 1). Radicipes has a wide distribution along the slopes in cold, deep water in the western and central Atlantic. It had not been observed in Norway until the MAREANO mapping programme found relatively dense concentrations of this sea whip at 800 m depth in the area known as the Bjørnøya slide (Buhl-Mortensen et al. 2015b). Another group of corals that may be regarded as member of the soft-bottom CG are the unattached solitary scleractinians. These may constitute “cup-coral fields” commonly comprised of specimens of the solitary coral Flabellum spp. (Caryophyllidae), at various depths from ~150 m and below, depending on the temperature of bottom waters. This soft-bottom CG is quite widespread and occurs, for example, on the shelf both off Nova Scotia (western Atlantic) and Norway (eastern Atlantic).

Hard-bottom CGs often occur in locations where currents are generally quite strong (with maximum current speeds exceeding 1 knt) and the sea bottom is hard.
They may be characterized by gorgonian or antipatharian species occurring in stands. The most common CWC species in the Northeast Atlantic, making up hard-bottom CG, are Paragorgia arborea, Primnoa resedaeformis, Paramuricea placomus, and Swiftia spp. Antipatharians are also common key species within hard-bottom CG in the central part of the North Atlantic Ocean, south of the Wyville-Thompson ridge, along the mid-Atlantic Ridge and along the north West Atlantic margin (Mortensen et al. 2008; Bullimore et al. 2013). However, Antipatharians are not observed in the Norwegian Sea. Although there is less biodiversity associated with the various corals comprising this biotope than associated with CWC reefs, they often sustain a large number of individuals and host-specific species that are not found in other biotopes (see chapter “Corals as Architects of the Oceans”).

There are few cold-water scleractinians that build reefs (see chapter “Global biodiversity of cold-water coral reef ecosystems” and “Framework-forming Scleractinian Cold-water Corals Through Space and Time: A Late Quaternary North Atlantic Perspective”), and based on current knowledge, one of these (Lophelia pertusa) is far more common than the rest. These mainly occur in the North Atlantic Ocean (e.g., along the Norwegian shelf, around the Faroes, the Logachev mounds, and the Porcupine Bank) and the Mexican Gulf. The number of verified Lophelia reefs off Norway (>1,200 verified and >6,000 indicated from detailed bathymetry) increases rapidly as the Norwegian habitat mapping program MAREANO proceeds (www.mareano.no), and it is clear that the shelf off Norway represents a core area for this species, almost at the end of the “Gulf Stream.”

Many colonial scleractinians do not form reefs, and reef-forming species such as Lophelia pertusa may occur in assemblages without presenting the characteristics of a reef. These may be termed “scleractinian gardens.” Scleractinians may grow on vertical solid substrates, such as bedrock walls on seamounts, in canyons and in fjords, as well as on human made structures such as oil rigs. On a vertical substrate,
coral debris cannot aggregate, and therefore reefs will not develop. *L. pertusa* gardens on steep substrate have been documented from the steep slopes around the Azores (Marina Carreiro-Silva IMAR/DOP, University of Azores, pers. comm.), the French, and Spanish Mediterranean canyons (Orejas et al. 2009) and the Whittard Canyon in the Northeast Atlantic (Huvenne et al. 2011). Off Galicia (Spain), “forests” of *Dendrophyllia ramea* are found on infralittoral and circalittoral bottoms and *Dendrophyllia cornigera* on circalittoral and bathyal rocky bottoms (OCEANA, pers. comm.). *D. cornigera* is found down to 600 m depth, whereas *D. ramea* occurs down to ca 150 m depth. Whereas *Lophelia* reefs are found near the west coast of Scotland (the Mingulay Reef Complex), Howell (2010) and Bullimore et al. (2013) have observed and described scleractinian CG west of Scotland, characterized by discrete colonies of *L. pertusa* and *M. oculata* and solitary scleractinians (*Caryophyllia* sp.) on hard substratum. In this chapter, we regard these as varieties of discrete scleractinian colonies on hard substratum.

2 Trophic Ecology

2.1 Framing Environment

The biological value of the trophic support and habitats provided by the cold-water host coral for the marine ecosystem depends on the surrounding habitat matrix, or what may be termed the “framing habitat” (Buhl-Mortensen et al. 2010). The framing habitat or surrounding environment is an important source of modifications of the communities of CWC forests. In locations where the framing environment is deep-sea soft sediments, the hard substrate offered by exposed coral skeleton represents a scarce habitat resource, offering a locally unique opportunity for sessile filter feeders to colonize. This habitat will often be colonized by species that are not common in the surrounding area and they are therefore often local hotspots of activity and diversity. *Lophelia pertusa* larvae are motile for extended periods of time (Larsson et al. 2014), and often larvae are to be found in suspension but unable to settle successfully due to less than optimum substrate conditions. On the deep-sea floor, commonly comprising of vast regions of soft sediment/low current environments, the occurrence of an area of firm substratum elevated into higher flow velocity waters will provide a habitat and stepping stone for sessile filter feeders. The presence of CWC forests and solitary suspension feeding megafauna may thus be a significant factor for the trophic ecology of a wider area than just within colonies.

2.2 Food Transport by Near-Bottom Currents

The near-bottom transport of food particles is vital for all benthic organisms, with delivery dependent on benthic boundary layer (BBL) conditions. The BBL is the zone of water which transports particulates immediately above the seafloor (see
Riisgard & Larsen in this volume). Within the BBL, a strong gradient of energy, dissolved and solid chemical components, suspended matter, and fauna may be found (Boudreau and Jørgensen 2001; Perlin et al. 2005) (Fig. 2). The BBL is not a physically distinct layer but is defined as the interface between the surface of the solid seafloor and an arbitrarily layer a selected distance away from the surface, where the shear effect on flow becomes “negligible” (Boudreau and Jørgensen 2001). The BBL is subdivided into a very thin “diffusive boundary layer and a viscous layer” a few millimeters thick, dominated by molecular viscosity and turbulence generated by the water body passing over the roughness of the seafloor and a “logarithmic layer.” The logarithmic layer is comprised of waters in which the velocity profile is represented by a logarithmic increase in flow velocity with distance from the seafloor. In deep-sea environments with slow currents and fine sediment in suspension, the BBL is narrow, whereas in the high-current environments of shallow waters, the BBL may comprise a larger part of the water column (Souza and Friedrich 2005).

The general pattern of decreasing BBL thickness and corresponding decrease in food particles availability at increasing depth implies that a slight elevation of even just a few centimeters above the soft-bottom, deep-sea seafloor into the logarithmic region of the BBL may well result in a marked change in the quantity and composition of suspended food available. Higher living structures, such as gorgonian corals, elevated into the laminar currents above the more turbulent near-bottom BBL may obtain other food sources (e.g., zooplankton) (Fig. 2) (Mortensen and Buhl-Mortensen 2005).
2.3 Feeding in Cold-Water Coral Forests

For coral forests to develop, sufficient substrate and food must be available at a location to allow for successful larval settlement and coral growth to occur. CWCs display a great variety of growth morphologies that aid their suspension/filter feeding (see chapter “Corals as Architects of the Oceans”). Growth morphology is quite flexible in some species and can vary in response to food availability and environmental conditions to maximize colony fitness in a particular location. Given a hard substrate and sufficient food, *Lophelia pertusa*, for example, can over successive generations form reefs tens of meters in height, of densely packed coral polyps, such as these occurring in larger reefs in Norwegian waters. *L. pertusa* growth morphology may vary in response to suspended inorganic particulate concentrations. Given a less abundant food supply, though a similarly suitable seafloor habitat, *L. pertusa* can form low height thickets of individuals, subsisting but with colonies not thriving or resulting in vertical reef-like growth.

Hydrodynamics in the vicinity of the seafloor are greatly influenced by surface roughness and topography. The development of coral reefs and gardens increases 3D complexity, with the development of the habitat both responding to and in turn influencing the hydrodynamic conditions present. Large developed reefs, such as in the Sula reef complex off Norway, commonly consist of a cap of live corals, with living polyps on all sides around the reef mound supplied by suspended food particles coming from different directions during the tidal cycle. The “dead” zones of these reefs are commonly characterized by reduced flow velocities. The reduced flow velocity conditions at the lower part of the reefs does allow some transported material to settle from suspension, supporting other filter feeders colonizing the “dead” coral facings, such as brittle stars, anemones, and hydroids.

In locations with near uniform current flow direction and high velocity currents, extended “cigar reefs” may form. Over time, successive generations of corals move in an upstream direction, with downstream corals slowly being staved of material for growth. These reefs, such as found at Traena and off Vesterålen (Norway), consist of small front sections of *Lophelia pertusa* interspersed with other suspension feeders such as the bivalve *Acesta excavata*, a fringe of gorgonian corals and transient *L. pertusa* growth and a tail section of less abundant corals (Fig. 3).

Temperature may well be a major factor in determining the amount of food a coral has to capture in order to thrive and for a species to contribute to a CWC animal forest (see chapter “Animal Forests of the World: an overview”). Experimental work has to date only been carried out with a few species, though for the key reef-forming coral *Lophelia pertusa* it seems small changes in temperature correlate with large changes in coral respiration (Dodds et al. 2007; Hennige et al. 2015). This would indicate that for a particular temperature sensitive species to continue to flourish in warmer waters, a higher abundance of suitable food would need to be supplied. From laboratory prey capture studies conducted with corals collected from the Norwegian fjord reefs and the warmer Mediterranean canyon, this would seem to be the case. Prey capture rates of *L. pertusa* polyps collected from the ~7 °C fjords in Norway capture roughly 10% of what polyps collected from the ~15 °C Mediterranean
canyons capture, all other conditions being equal (Tsounis et al. 2010; Purser et al. 2010).

Feeding mechanisms of CWCs within animal forests vary, both by coral species and food type. It seems likely that mucus entrapment and digestion of prey outside the coral polyp occurs in some species (Wijgerde et al. 2011). In others, mucus may be used to capture material from suspension, perhaps after increasing local turbulent flow conditions as a result of polyp tentacle extension, then retracting this mucus and entrapped food into the polyp (Wijgerde et al. 2012). For prey of a suitable size, or motile prey items, *L. pertusa* use polyp tentacles directly to catch food. For small or motionless particles tentacles are not used (moved) but the food is transported by ciliary motion on the tentacles’ surface (Mortensen 2001). There is also the indication that dissolved material within bottom waters may be utilized directly by corals (e.g., Mueller et al. 2014). Some species may employ these methods to varying degrees, as the environment and food availability dictates, though other factors, such as coral polyp spacing, polyp distance from seafloor, and prey capture surface area, also influence suitability of a particular niche for colony growth.

Recent experimental work and in situ observations with high temporal resolution instruments indicate that the long reported paradigm that CWC species best capture prey under environmentally high flow conditions may not be wholly, or in the case of all species, correct. For *Lophelia pertusa*, it has been observed that flow velocities in areas of high abundance may often be higher than in adjacent, sparsely inhabited regions of seafloor. However, these currents seldom exceed 25 cm s$^{-1}$. The currents commonly show tidal variations with periods of velocities below 10 cm s$^{-1}$. Higher flow provides an increased flux of food. However, it may also complicate prey capture by deforming feeding apparatus, rendering feeding mucus less effective, and detaching recently captured or partially digested food. Also, it may deliver elevated concentrations of undesirable, refractory material. Similar mechanisms have been described for shallow-water octocorals. In the laboratory, *L. pertusa* collected in the
NW Mediterranean canyons have been shown to capture prey most effectively at velocities of 5 cm s\textsuperscript{-1} (Tsounis et al. 2010) and specimens from the Norwegian fjord at 2.5 cm s\textsuperscript{-1}. From fieldwork conducted at the Mingulay Reef (Scotland) and the Tisler Reef (Norway), such reduced current velocities may occur as tidal direction changes, with higher flow conditions prevalent for much of the tidal cycles (Davies et al. 2009). At the periods with strong currents, polyps may retract into the calyx (skeletal polyp houses) until the current slows down and the feeding conditions are favorable again. At Mingulay at least, this reduction in velocity is associated with increased food availability at a CWC reef site (Duineveld et al. 2012). There are indications that this might also be the case at the Tisler Reef (a sill reef in Norway, just north of the border to Sweden).

Corals are “messy” feeders. A percentage of food removed from suspension by whichever feeding mechanism is employed will not be ingested by the individual polyp. The mucus produced by cnidarians for cleaning and prey capture can be resuspended by currents or “drip” from the generating organism, taking with it any embedded food. This material may be transported downstream and out of the animal forest environment be redeposited or recaught by other corals, or be delivered to the complex microhabitat formed amongst coral branches, in the case of scleractinian reef-forming corals. Further, food trapped by CWC corals can be utilized by associated organisms. In the case of both gorgonian and scleractinian corals, shrimp can be commonly present in locally elevated abundances on living coral colonies, with their patterns of distribution perhaps determined by polyp spacing, as they grab entrapped food from their hosts. Amphipods are common and abundant on many gorgonians and likely also benefit from secondhand food delivery, either directly from entrapped material or from suspension in the locally lowered flow velocity conditions associated with the coral branching (Buhl-Mortensen and Mortensen 2004a).

3 Cold-Water Corals as Habitat Providers and Biodiversity Hot Spots

Individual CWC colonies, be they gorgonian, scleractinian, or antipatharian, have been shown to support numerous associated species, with species richness and individual numbers within and surrounding coral branches found to be in some cases orders of magnitude higher than in surrounding seabed (see chapter “Corals as Architects of the Oceans”). With sufficient corals present to allow the ecosystem to be characterized as an animal forest habitat, this boost to local species richness and biomass support is further increased by the physical provision of additional habitat niches. The understanding of the trophic support of CWC animal forests must rely on knowledge of the associations between other species and CWC.

At a local scale, colony morphology shapes the environment by modifying the hydrodynamics, providing shelter against strong currents, and facilitating local deposition of particulate matter (Table 1). Such local environmental conditions are extremely difficult to study in situ in the deep sea. Therefore, indices calculated from
architectural attributes can be used to explain structural differences between biotic agents. Such descriptors include size (height and width), volume (total, between branches or in canals), surface area, and branching patterns (meander system, fractal description, etc.). The flexibility of the biotic substrate is another factor which affects epibionts, similar to the effect of sediment grain size on substrate stability.

CWC forest habitats are, as already mentioned, numerous in type. However, most studies of CWC associated fauna have focused on *L. pertusa* (Jensen and Frederiksen 1992; Mortensen 2001; Mortensen and Fosså 2006; Henry and Roberts 2007; Purser et al. 2013), whereas few have focused on other CWC species (Buhl-Mortensen and Mortensen 2004a, 2005; Mosher and Watling 2009; De Clippele et al. 2015). The term “associated fauna” here is used to describe any animal found on or in a coral colony. Corals have a complex architecture that offers a great variety of microhabitats for other organisms, and provides substrata of different ages, and different stages of colonization (see chapter “Corals as Architects of the Oceans”).

CWCs provide physical niches in terms of suitable substrate for sessile epifauna, or the coral skeleton and tissues may be inhabited by cryptofauna (hidden inside the skeleton) or endoparasites (e.g., arthropods, nematodes, fungi, or sponges). Sheltered cavities within a colony can contain organically rich sediments, while outer parts provide high water flow with little sedimentation smothering risk. The tree-like morphology of most corals allows their polyps to be elevated from the relatively still boundary layer close to the substratum into the faster flowing waters above (Wainwright and Koehl 1976). In addition, the orientation of colonies perpendicular to prevailing currents, which is common for many species, maximizes the volume of water passing the polyps (Wainwright and Dillon 1969; Mortensen and Buhl-Mortensen 2005). This enables the polyps in the colony to have maximum food access, an advantage that is passed on to any filter-feeding epizoic animal associated with the colony.

| Table 1 | Habitats and resources provided by major biotic habitat-forming taxa (From Buhl-Mortensen et al. (2010)) |

<table>
<thead>
<tr>
<th>Biotic habitat</th>
<th>Available habitat</th>
<th>Resource for associates</th>
<th>Detritus trapped</th>
<th>Predator protection</th>
<th>Food</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Lophelia</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Live</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dead</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Rubble</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>Gorgonians</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Live</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Dead</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Seapens</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Glass sponges</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Demospongia</td>
<td>—</td>
<td>x</td>
<td>x</td>
<td></td>
<td>x</td>
</tr>
<tr>
<td>Xenophyophoridea</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
</tbody>
</table>
Branches of living corals can be foci for use by many invertebrates, which may either collect food directly from coral polyps or use the structure as a means to attaining a greater elevation in the water column (e.g., basket stars, galatheids, isopods, shrimp). Dead coral framework from gorgonians/antipatharians may provide suitable refuges for mobile fauna, such as galatheid crabs, shrimp, and small fish.

The structure of the corals, and the close proximity of colonies within a CWC forest, provide a range of turbidity regimes and flow patterns which may support a range of associated species. In low flow regions, fauna subsisting on small particulate material or dissolved material may find suitable habitats, whereas closer to the leading edge of forests or the peaks of colonies, areas of high flow and/or nutrient entrapping turbidity loops may be present. These two contrasting habitat niches may be separated within a CWC animal forest by just a few tens of cm, one of the many examples of high habitat heterogeneity in CWC forests.

As forests develop over time, coral colonies can grow or die off, as a consequence of nutrient delivery, external damage, environmental change, senescence, etc. These changes have a knock on effect on the flow conditions of a habitat and therefore there are temporal variations in the suitability of niches to various organisms. Extreme environmental changes have happened in the past during and following glaciation events when change in sea levels, as well as the change in food delivery following ice retreat, has been proposed as a factor in the waxing/waning of CWC animal forests on seamounts on the Irish margin (Rüggeberg et al. 2007). Areas at one time highly suitable for CWC animal forest development may become less optimal over a scale of centuries.

Trophic support and habitat provision differ with coral species and age of the host. Small species with no exposed skeleton, e.g., sea pens and broccoli corals, offer few habitats (De Clippele et al. 2015) whereas larger species with more complex branching patterns allows for provision of a greater number and diversity of habitats (Buhl-Mortensen and Mortensen 2005). As the host grows larger and older additional habitats are provided, e.g., pockets of detritus and exposed skeleton in old parts of the colony, and provision of access to elevated location with stronger currents and a higher food flux to the upper and outer parts of the colony (Table 2 and 3). Below we present the general characteristics of associated fauna for three main types of CWC forest (sea pen stands, hard-bottom coral gardens, and Lophelia pertusa reefs) separately.

### 3.1 Sea Pen Stands

It seems like the fauna on sea pens in general is less abundant and diverse than for gorgonians (De Clippele et al. 2015). Sea pen associates are dominated by shrimps and ophiuroids, which use the sea pens as shelter and/or as feeding platforms (De Clippele et al. 2015). A role as nursery habitat for redfish has also been suggested (Baillon et al. 2012). The ophiuroid *Asteronyx loveni* is most common on *Funiculina quadrangularis*, which is used as a platform to reach better feeding conditions. The squat lobster *Munida sarsi* is often observed close to the sea pen *Kophobelemnon stelliferum* which presumably offers shelter against predators.
Table 2 Overview of microhabitats provided by major biotic habitat-forming taxa and water masses where they mainly occur. X: most common. X: less common (From Buhl-Mortensen et al. (2010))

<table>
<thead>
<tr>
<th>Habitat</th>
<th>Protista</th>
<th>Porifera</th>
<th>Octocorallia</th>
<th>Scleractinia</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Xeno</td>
<td>Hexact</td>
<td>Demo</td>
<td>Calc</td>
</tr>
<tr>
<td>Live tissue</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Inside</td>
<td></td>
<td></td>
<td>X</td>
<td>x</td>
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<tr>
<td>Outside</td>
<td>x</td>
<td>x</td>
<td>X</td>
<td>x</td>
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<tr>
<td>Exposed skeleton</td>
<td></td>
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<tr>
<td>Inside</td>
<td></td>
<td></td>
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<tr>
<td>Outside</td>
<td>x</td>
<td>X</td>
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<tr>
<td>Sheltered space</td>
<td></td>
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<td></td>
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<tr>
<td>Cavities</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
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<tr>
<td>Canals</td>
<td>x</td>
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<tr>
<td>Water mass (depth)</td>
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<tr>
<td>Shallow</td>
<td>x</td>
<td>x</td>
<td>X</td>
<td>x</td>
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<tr>
<td>Intermediate</td>
<td>x</td>
<td>x</td>
<td>X</td>
<td>x</td>
</tr>
<tr>
<td>Deep</td>
<td>x</td>
<td>X</td>
<td>X</td>
<td>x</td>
</tr>
</tbody>
</table>

Xeno xenophyophoroidea, Hexact hexactinellida, Demo demospongia, Calc calcarea, Penna pennatulacea, Alcyo aleyonaria, Gorgon gorgonacea, Soli solitary, Col colonial

Table 3 Overview of habitat aspects (size, substrate flexibility, and 3-D complexity) of major biotic habitat-forming taxa

<table>
<thead>
<tr>
<th>Size</th>
<th>Medium (25–300 cm)</th>
<th>Large (&gt;3 m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Small (&lt;25 cm)</td>
<td></td>
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</table>

Substrate flexibility

| Rigid                  | Solitary scleractinians, Xenophyophoroidea (some) | Colonial Scleractinia | Reef-forming scleractinians |
| Flexible               | Porifera, Gorgonacea, Antipatharia, Porifera, Gorgonacea | Porifera, Gorgonacea | Reef-forming sponges |
|                        | Pennatulacea, Xenophyophoroidea | Antipatharia, Pennatulacea | Reef-forming sponges |
| Soft                   | Porifera, Alcyonaria, Xenophyophoroidea | Porifera, Alcyonaria | |

Complexity (surface/volume)

| Low                    | Sponges, Gorgonacea | Sponges, Gorgonacea |
| Medium                 | Solitary scleractinians | Sponges, Pennatulacea, Gorgonacea |
| High                   | Xenophyophoroidea | Colonial Scleractinia | Reef-forming scleractinians |

Off the Norwegian coast, De Clippele et al. (2015) observed 12 taxa on four sea pen species (*F. quadrangularis*, *Pennatula phosphorea*, *Virgularia mirabilis*, and *K. stelliferum*) and report that only a small proportion (5%) of studied colonies
having associated fauna. However, a greater proportion (15%) of the colonies had organisms such as the squat lobster, *Munida sarsi*, occurring in close proximity.

The association between the *A. loveni* and *F. quadrangularis* is probably an example of obligate commensalistic relationship, which is relatively common for brittle stars and octocorals (Buhl-Mortensen and Mortensen 2004a; Mosher and Watling 2009). De Clippele et al. (2015) found that *Funiculina quadrangularis* was the only sea pen that hosted this brittle star, which occurred as solitary individuals on 7.5% of 278 inspected colonies. Only one colony hosted two individuals. The brittle stars were found predominantly on the central or upper parts of the colony with only two specimens observed in the lower part of the colony. Most individuals extended one to four arms out from the colony.

### 3.2 Hard-Bottom Coral Gardens

The widespread cold-water gorgonians *Primnoa resedaeformis* and *Paragorgia arborea* host a rich fauna in the Atlantic. *P. resedaeformis* is a bush-forming coral that can occur in dense tickets on rocks and boulders. Maximum height is around 1 m, which a colony would need at least 70 years to reach. This coral deposits annual rings within its skeleton, just like a tree, which can be used to determine the age of the colony (Sherwood and Edinger 2009) (see also chapter “Growth Patterns in Long-lived Benthic Suspension Feeders”). A parasitic anemone (*Epizoanthus* sp.) can take over the skeleton of this coral when the skeleton is exposed due to tissue damage (Fig. 4). The anemone, which has been mistaken for a coral, can cover whole

![Fig. 4](Image courtesy: Bjørn Serigstad, Institute of Marine Research, Norway)
colonies. The anemone received an increase in three-dimensional space from the coral skeleton, together with better access to food particles. *P. arborea* forms larger “trees,” white, pink, or red in color on boulders or bedrock. This gorgonian can reach a height of at least 2 m. A coral of that size is probably more than 100 years in age (Mortensen and Buhl-Mortensen 2005).

Many associated species thrive on the corals or in their vicinity. Basket stars (*Gorgonocephalus lamarckii*, *G. eucnemis*, and *G. caputmedusae*) can be found on the outer branches of *Paragorgia* (Fig. 5). This is a brittle star belonging to the group Gorgonocephalidae (“Gorgon-headed”), which is named after the snake-haired sisters of Greek mythology. The basket star snags plankton and other organic particles in its canopy of branching arms and ushers them to its mouth on the underside of the center disk. Redfish (*Sebastes* spp.) are often hiding amongst the coral colonies. These fishes often have prolonged periods of resting on the bottom when they need to hide from predators and strong currents.

The cold-water gorgonians offer different microhabitats for both sessile and mobile invertebrates. Buhl-Mortensen and Mortensen (2005) identified two main types of microhabitats on the colonies: “Habitat 1,” young parts of the colony covered with live tissue and “Habitat 2,” old or dead parts of the colony with detritus deposits and exposed skeleton.

### 3.2.1 *Paragorgia*

**Habitat 1**

Young and live substrate. Organisms are found both on the surface of the colony and inside the polyps or skeleton. In general few species are associated with this habitat, and the most common organisms are parasitic copepods. On the surface, a parasitic lichomolgid copepod may occur in hundreds on a single
colony. Inside polyps on the branches of outer parts of the colonies a lamippid copepod, *Gorgonophilus canadensis* lives endoparasitically (Buhl-Mortensen and Mortensen 2004b). The copepod induces malformation in the producing gall-like structures containing egg sacks, large females, and several smaller males. The echinoderm *Gorgonocephalus lamarckii* seems to be associated with high velocity current to which the branches of *P. arborea* are exposed. *G. lamarckii* specimens on *P. arborea* are predominantly large individuals with disc diameters of 1.5–6 cm. Buhl-Mortensen and Mortensen (2004b) observed 15 individuals on one large *P. arborea*. Various sea anemones may also be attached to the colony branches and polynoid polychaetes occasionally observed clinging firmly to the surface of the coral.

**Habitat 2**

Old and dead substrate. Here, particulate deposits are commonly observed between the basis of branches. In these parts of the colony, with thick branches, the pigmented outer living tissue can disappear and the spongy, pale skeleton is exposed. Organisms may be found both on the surface and within the skeleton of the coral. Polychaetes belonging to the families Sabellidae, Nereidae, and Polynoidae may be present in burrows within the skeleton. In detritus laden areas, the amphipod *Ischyrocerus megacheir* may use the organic particles to build nests. Hydroids are sometimes found close to the center of the fan-shaped colonies, attached to small areas of exposed skeleton. The hydroids in turn are hosts to a number of secondary associates such as cirripeds, foraminifers, amphipods, ostracods, isopods, and mites.

### 3.2.2 Primnoa Resedaeformis

**Habitat 1: Young and Live Substrate**

In this species as well, associated species can be found both on the surface of the colony as well as inside the polyps. In general, species richness of this habitat is quite low. The shrimp *Pandalus propinquus* may be found on the branches and mites can be observed on close examination on the surface. The parasitic lamippid copepod *Enalcyonium cf. olssoni* probably living inside the polyps is frequently encountered. Male and female decapods (*Dorhynchus thomsoni*) have also been reported in this habitat.

**Habitat 2: Old and Dead Substrate**

In *Primnoa*, this habitat is represented by its hard-exposed skeleton which is the substratum for many sessile epizoans. The skeleton is often colonized by hydroids, molluscs, bryozoans, foraminifers, and cirripeds. A parasitic anemone, *Epizoanthus*
sp., sometimes covers large parts of the skeleton in the western Atlantic. Amphipods and isopods are often found amongst hydroids, together with the cirriped Ornatoscalpellum stroemii. A rich fauna of foraminifers occur in this habitat, some of which are attached to the hydroids. Several bivalves (especially Anomidae and Pectinidae species), cirripeds, and bryozoans also often occur attached to the coral skeleton. The exposed skeleton may also be colonized by octocorals such as smaller and more rare gorgonians.

4 Cold-Water Coral Reefs

Of all CWC fauna, the framework forming scleractinian species have been the most extensively studied, particularly L. pertusa, the most abundant framework forming coral in European waters (see also chapter by Henry & Roberts and by Wienberg et al. in this volume). However, this species is common elsewhere in the Atlantic Ocean, and studies are being undertaken in regions where this coral was little known such as western Africa (Le Guilloux et al. 2009). Figure 6 illustrates that CWC reefs off Ghana display many similarities with Lophelia reefs from the Northeast Atlantic.

The framework forming species can produce sizable calcium carbonate structures over time, with overall morphology dependant on seafloor composition and substrate, regularity of flow direction, food abundance and food quality, as well as a host of other environmental conditions. In these highly complex ecosystems, a number of microhabitat categories can be identified, each providing useful

Fig. 6 The Basket star (Gorgonocephalus sp.) uses the coral to get access to food particles (Photo courtesy: MAREANO/Institute of Marine Research)
niches for a range of organisms. Below we present the two main habitats within CWC reefs.

### 4.1 Habitat 1: Live Coral Zone

Commonly in scleractinian CWC reefs, a distinct region of the structure is thickly covered with live coral polyps. This is usually the area most regularly exposed to freshly transported nutrients in suspension, i.e., facing into the prevailing current (Fig. 7). Where current direction is near uniform, “cigar” shaped reefs may form (Buhl-Mortensen et al. 2010), whereas in locations with more varied current flow conditions, this living reef habitat may form the flanks of seamounts or the crests of coral ridges. In contrast to shallow-water scleractinian reefs, CWC reefs are formed by one or few scleractinian species in a particular location. The live reef habitat is a useful area to colonize or utilize for filter feeders requiring exposure to elevated currents, and several species of fish, shrimp, and various other arthropods may occupy the coral surface to reach higher flow conditions. Protected by a thin layer of living tissue (coenosarc) sessile filter feeders find colonization of this habitat difficult, though damage to the reef can expose skeleton to colonization by the gorgonians *Paragorgia arborea* and *Primnoa resedaeformis* (as well as other filter feeders such as hydroids and bivalves, e.g., *Acesta excavata*) and the sponge *Mycale lingua* in European waters (Purser et al. 2013), with other species occupying such locations elsewhere in the world ocean.

![Fig. 7](image_url) Animal forests often occur as a mosaic of habitats, and on the *Lophelia* reefs off Norway, the gorgonian *Paragorgia arborea* commonly occur in higher densities than in other habitats. The orientation of the colonies indicate the main prevailing current direction. Here this is especially evident in the red *Paragorgia* colony, growing in the middle of a live *Lophelia* colony (Photo courtesy: Institute of Marine Research, Norway)
4.2 Habitat 2: Dead Coral Zone

As a scleractinian reef develops the living fringe of coral is overgrown by subsequent generations better placed to extract material from the water column. Previous generations die, presumably due to reduced water flow and food supply, with retreating coenosarc coverage opening the skeleton to colonization. As mentioned for gorgonian corals, these exposed skeleton regions offer opportunity for internal colonization of structures by parasitic sponge, fungi, and anemones, with these organisms extending internally within the coral structure to attack still-living polyps. The skeleton also provides structural refuges for fish and other mobile fauna and provides substrate for colonization of sessile suspension feeders. This part of the reef is the most diverse, with microhabitats of coral skeletons at various ages, allowing for simultaneous presence of parallel successions of communities (Fig. 8). Commonly, the upper regions of dead coral, close to the live coral zone, are preferentially occupied by suspension feeders such as hydroids and anemones.

4.3 Habitat 3: Rubble Zone

Following death, the coral structure is slowly degraded by physical and biological action, and depending on local conditions, a potentially extensive region of seafloor surrounding habitats 1 and 2 can become covered in a mix of broken coral fragments and deposited sediments. This can provide a range of habitat niches for infauna and

Fig. 8 The diversity of species is highest in the dead coral matrix zone of CWC reefs. Here live *Lophelia* also occur but much less extensive than in the live zone. New surface from dying corals are constantly made available to new settlers, and new and old substrates are found side by side (Photo courtesy: Institute of Marine Research, Norway)
sessile filter feeders. In areas downstream of CWC reefs colonization by ophiuroids, soft corals, sponges, anemones, or other filter feeders can be extensive. The rough topography of this habitat provides turbulent bottom flow conditions, which allow for regular resuspension of entrapped materials.

5 Cold-Water Coral Forests as Feeding Place and Nurseries for Fish

The majority of studies of fish in coral forests suggest that the presence of CWCs supports high abundance and diversity of fish assemblages, whereas some studies report that the existence of such a relationship is ambiguous (Biber et al. 2014). Coral forests provide habitat for associated fish species and support high diversity and abundance of potential prey species for fish (Mortensen et al. 2005) Kutt et al. (2014) report a generally higher abundance of fish in and around Norwegian CWC reefs, but they also point out that these elevated populations are transient, and that the habitats do not seem to be essential for most commercial and observed fish species. A similar pattern is also reported from Mediterranean CWC reefs and adjacent habitats (D’Onghia et al. 2012) – utilization being opportunistic rather than essential within the lifecycle of the fish. There are not many studies on the diet of fish in coral forests, but Husebø et al. (2002) compared the stomach content of redfish (Sebastes marinus), tusk (Brosme brosme), and ling (Molva molva) caught on reefs with the same species caught in other habitats. They report that these fishes tend to be larger on the reefs. The diet of the three fish species included the same prey groups in all habitats, but prey differed at the species level.

Tusk is common on NE Atlantic CWC reefs, utilizing small caves in the coral framework, in which to rest, hide, or prepare ambush attacks on potential prey. Whereas tusk seem to be using reefs as their preferred feeding habit, redfish are more likely to use the reefs as a resting place to ride out periods of strong currents. There are indications that zooplankton and other particles are concentrated over CWC reefs (Mienis et al. 2014). For redfish, these potential prey organisms are not available during the periods of a tidal cycle when the current is at its strongest. During such times the fish can be observed resting between coral colonies. During slack tide, however, the redfish can be observed up in the water feeding on larger zooplankton (Dons 1944, Buhl-Mortensen et al. 2015a).

Ray eggs are often found on gorgonian corals where they are firmly fastened and receive a high flow-through of oxygenated waters (see also chapter “Global Biodiversity in Cold-Water Coral Reef Ecosystems”). Figure 9 shows a colony of Paragorgia arborea with 26 eggs of deep-sea catshark (Apristurus profundurum). As mentioned previously, sea pens have been found with red fish larvae attached (Baillon et al. 2012). Juvenile fish have not been commonly observed in coral forests but there is a chance that this is an underrepresentation if the juvenile fish lives largely cryptically. There are many reports of juvenile basket stars (Gorgonocephalus spp.) amongst the branches of the so-called broccoli corals (Fig. 10) (Mortensen 1927; Buhl-Mortensen and Mortensen 2004a), hiding from
predators in an elevated position from the seafloor and also benefitting from increased flux of suspended food particles.

6 The Role of Symbionts

Symbionts are species that are restricted to association with certain taxa for their existence. These could be parasites, commensals, or mutualistic symbionts. The composition of associated fauna is in general not host specific but consists mainly of species also occurring in other habitats. Exceptions are a few highly specialized parasites. Most associated species use the corals as substratum or refuge with few utilizing the coral as a food source.

Polynoidae (Polychaeta) is the most common family of symbiotic polychaetes on CWCs. Many of the species are obligate to antipatharian and gorgonian corals (Buhl-Mortensen and Mortensen 2004a). One peculiar example of such symbiosis is the polynoid Harmothoe oculinarum living on Lophelia pertusa, often inside tubes of
the polychaete *Eunice norvegica* (Jensen and Frederiksen 1992; Mortensen 2001). The polychaete is bright white and blends in with the coral. *Eunice norvegica* commonly feeds on food particles captured by the coral’s polyps (Mortensen 2001). However, it also exhibits behavior which is highly beneficial to the coral, by cleaning the coral surface and attacking invading mobile organisms (Mortensen 2001). Furthermore, it stimulates the coral’s calcification processes (Mueller et al. 2013). The enhancement of calcification is also thought to strengthen the coral skeleton. *E. pennata* and *E. dubiata* are reported as facultative kleptoparasitic commensals or mutualists on *Madrepora oculata* (Martin and Britayev 1998). Another example of obligate mutualistic symbiont is the polychaete *Haplosyllis anthogorgicola*, which is reported from the gorgonian species *Anthogorgia bocki* in the Japanese seas (Utinomi 1956). *Lumbrineris flabellicola* is perhaps the polychaete with the widest array of coral hosts in deep water. It is an obligate commensal on cnidarians, mainly scleractinians, but also occurs on unidentified hydroids and zoantharians (Zibrowius et al. 1975). It has been recorded on 22 scleractinian species in the Pacific and Indian Ocean (Miura and Shirayama 1992; Zibrowius et al. 1975; Cairns and Zibrowius 1997).

7 Coral Associates in Cold Versus Warm Waters

Corals in the cold deep are obviously lacking zooxanthella (symbiotic algae), which are so characteristic for warm shallow-water coral reefs. This also reflects a big difference in trophic structure with implications for the composition of functional
Obligate associations between species are rare among associates with cold-water scleractinians, a great contrast to the many examples of symbiotic associations between various taxa and reef-building corals in warm water. Interestingly, there are more examples of obligate association for octocorals than for hexacorals (the reef builders) in cold water. The fauna associated with CWC consists mainly of sessile suspension feeders. However, there is also a rich associated mobile fauna consisting of both deposit feeders and predators. For cold-water gorgonians, this fauna may be richer than what can be found on tropical gorgonians (e.g., Goh et al. 1999). This fauna is dominated by crustaceans both in abundance and number of species. The abundance and diversity of associated fauna is positively correlated to host morphology (e.g., number of branches and height of colony) both for warm-water gorgonians (Abele and Patton 1976) and cold-water gorgonians (Buhl-Mortensen and Mortensen 2005).

Buhl-Mortensen and Mortensen (2005) compared results on fauna associated between two species of cold-water gorgonians (P. arborea and P. resedaeformis) off Nova Scotia and 16 species of shallow-water gorgonians on coral reefs in Singapore (Goh et al. 1999). Characteristic for both warm- and cold-water-associated fauna was the dominance of amphipods and frequent occurrence of parasitic copepods. Interestingly, the associated fauna of the two cold-water gorgonians comprised more species and a higher abundance than of the warm-water associates. While the peracarid fauna seems to be richer on cold-water gorgonians, the decapod fauna on the tropical corals is richer than observed on the cold-water gorgonians. Some of the differences in observed faunistic composition might be due to sampling methods (SCUBA diving vs. ROV). However, for the decapods fauna the high number of associates of shallow-water tropical gorgonians probably reflects the high diversity of decapods in general in these waters. As mentioned above, many of the species associated with tropical corals are obligate (Patton 1972, and references therein), while most species found on the deep-water corals are facultative symbionts (Buhl-Mortensen and Mortensen 2004a). However, many of the species associated with the corals are much less common in other habitats. Several conditions of the North Atlantic deep-water coral habitat can be used to explain this general pattern, including time needed for development of such relationships, frequency of disturbance, and variability of nutrient supply. In general, interspecific obligate relationships are less common for high-latitude biotopes, compared to the tropics (Karr 1971; Rhode 1978; Beaver 1979). At present, CWC ecosystems have been less studied for tropical areas than areas at high latitudes. It is therefore uncertain whether the lack of obligate relationships in CWC forests simply is a false impression or this remains a fundamental difference between the warm and the cold coral ecosystems.

8 Conclusion

The diversity of CWC forests is great with respect to species composition of habitat forming and associated species, habitat heterogeneity across spatial scales, and trophic ecology. Even though the trophic ecology of CWC is not fully understood,
it is clear that they utilize a wide array of food sources, which partly explain the wide environmental range of their habitats. As the food supply to CWC forests rely largely on particulate matter transported by currents, the seabed topography is an important factor creating optimal conditions for particle concentration and retention for several types of CWC forests. Similarly, the morphology of CWCs and the habitats they develop is crucial for food supply for themselves as well as their associates. Tidal variation of current velocities seems to be important for creating “feeding windows” for species with different optimal current speeds for particle capture. The perceived image of cold-water coral ecosystems as less diverse, with few examples of obligate association between various species and their coral host, may not completely reflect the real picture. To reveal whether there is a fundamental coevolutionary difference between cold- and warm- coral ecosystems, more studies on CWC ecosystems in tropical waters are needed.

9 Cross-References

- Animal Forests of the World: An overview
- Benthic-Pelagic Coupling: New Perspectives in the Animal Forests
- Corals as Architects of the Oceans
- Ecosystem Functions and Services of the Marine Animal Forests
- Energetics, Particle Capture, and Trophic Ecology of Suspension Feeders
- Filter-Feeding Zoobenthos and Hydrodynamics
- Seston Quality and Available Food: Importance in the Benthic Biogeochemical Cycles

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