SPECIAL TOPIC

Biological structures as a source of habitat heterogeneity and biodiversity on the deep ocean margins

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Abstract

Biological structures exert a major influence on species diversity at both local and regional scales on deep continental margins. Some organisms use other species as substrates for attachment, shelter, feeding or parasitism, but there may also be mutual benefits from the association. Here, we highlight the structural attributes and biotic effects of the habitats that corals, sea pens, sponges and xenophyophores offer other organisms. The environmental setting of the biological structures influences their species composition. The importance of benthic species as substrates seems to increase with depth as the complexity of the surrounding geological substrate and food supply decline. There are marked differences in the degree of mutualistic relationships between habitat-forming taxa. This is especially evident for scleractinian corals, which have high numbers of facultative associates (commensals) and few obligate associates (mutualists), and gorgonians, with their few commensals and many obligate associates. Size, flexibility and architectural complexity of the habitat-forming organism are positively related to species diversity for both sessile and mobile species. This is mainly evident for commensal species sharing a facultative relationship with their host. Habitat complexity is enhanced by the architecture of biological structures, as well as by biological interactions. Colony morphology has a great influence on feeding efficiency for suspension feeders. Suspension feeding, habitat-forming organisms modify the environment to optimize their food uptake. This environmental advantage is also passed on to associated filter-feeding species. These effects are poorly understood but represent key points for understanding ecosystems and biodiversity on continental margins. In this paper we explore the contributions of organisms and the biotic structures they create (rather than physical modifications) to habitat heterogeneity and diversity on the deep continental margins.

Problem

Habitat complexity and heterogeneity have been linked to changes in organism abundance and diversity in a variety of terrestrial and aquatic settings (Bell 1985 and references therein; Levin & Dayton 2009). The ocean margin is characterised by topographical heterogeneity including varying slopes, sediment types and abiotic variables from the continental shelf edge at 200 m, down to abyssal plains at *c.* 4000 m depth. Depending on the sedimentary and current regime, the bed-rock can be covered by layers of sediment at different stages of

consolidation and dissected by canyons that act as channels for the transportation of material from the shelf to the deep sea. Transport events can be episodic, violent cascades leading to erosion and the deposition of material in the deep sea (Canals *et al.* 2006), imposing temporal and spatial variability on the fauna living in the region (Company *et al.* 2008). Generally, as depth increases within a well-oxygenated continental margin, there is a decrease in substrate variability, grain size, bottom current, food supply and size of epibenthic fauna that can provide structures as a source of habitat heterogeneity (Levin *et al.* 2001; Carney 2005). Superimposed on this abiotic background is the structure and heterogeneity generated by the presence of living organisms. Alteration of the physical environment by organisms has been termed 'ecosystem engineering' (Jones *et al.* 1994). All organisms must have some effect on their environment, but ecosystem engineering refers particularly to the non-assimilatory effects of an organism on its environment (Wright & Jones 2006). Indeed, the effects of the organism can persist after its demise, either as traces or as permanent skeletal remains. We focus here on biotic structures (skeletons, tests or tissues) rising above the sea floor in non-reducing ecosystems. We do not include the effects of 'engineers' working within the sediments, a vast topic beyond the scope of this review, nor do we consider the considerable engineering effects of tubeworm bushes, mussel and clam beds at vents and methane seeps that are reviewed by Cordes *et al.* (2010).

This paper considers the habitat heterogeneity provided by sessile organisms in the deep sea (200–4000 m) and the increased species diversity associated with it. The coverage is not comprehensive and the examples are drawn from the systems that the authors know best and mainly concern the North Atlantic. We focus on reef-forming organisms such as deep-sea scleractinian corals and sponges, more solitary colonial cnidarians (gorgonians and sea pens) and large agglutinating foraminifera, including xenophyophores. For each of these groups on deep-sea margins we address the following questions:
1 What types of biotic structures are provided that increase habitat heterogeneity?
2 What is the nature of the structural modifications?
3 How do these modifications influence the composition and diversity of associated faunas?

We then attempt to synthesize the relative degree to which obligate associations develop and the context-dependence of biogenic influences. We ask, do the influence of biotic groups and their interaction with surrounding ecosystems vary as a function of water depth, flow regime, food supply and oxygenation or predation regime? Finally, we consider how biotic structure heterogeneity interacts with human activities and climate change

to modify community structure and raise future questions in need of attention by researchers.

Terminology

For the purposes of this paper we will define *symbionts* strictly as organisms (microbes, protists or animals) mainly living inside or outside the tissues of other animals. We refer to organisms loosely associated with biotic structures as *commensals*, or as *mutualists* when the host and commensal both clearly benefit from the relationship. We will refer to the substrate made by structure-forming organisms (corals, sponges, xenophyophore tests) as *biotic substrate*, and distinguish these from biogenic substrate, which could include sediment features (burrows, mounds, *etc.*) not considered here.

Framing habitats of biological structures

The added habitat heterogeneity provided by biotic structures depends on the surrounding habitat matrix, or what we have termed here the 'framing habitats'. The ocean margins display several gradients (*e.g.* depth, water mass characteristics, current regime, sea-bed topography, sediment type, oxygenation and productivity) that influence the biodiversity to an extent that is not well understood for the deep sea (see Levin *et al.* 2001; Carney 2005).

The shelf/slope border (200–400 m)

The main features on the shelf/slope border are gravelly moraines, boulder fields, and banks intersected with troughs, where sediments vary from level muddy bottoms to shelly sand (Fig. 1) (Mortensen *et al.* 2009). Strong tidal currents, together with seasonal changes in temperature and wave energy, influence the habitats and generate large sand waves (Reynaud *et al.* 1999). Here, reef-forming organisms create large and complex structures that significantly increase habitat heterogeneity. Reefs of *Lophelia pertusa* (Frederiksen *et al.* 1992; Mortensen *et al.* 2001) (Figs 2 and 3), dense occurrences of large sponges (*e.g. Geodia* and *Isop*) (Fig. 4), and large gorgonian corals (Tendal 1992) (Fig. 5) can occur within narrow depth ranges. Framing habitats are varied and offer a wide range of substrates, but the complexity of these large structures represents an increased variety of micro-habitats that elevate local species diversity (Buhl-Mortensen & Mortensen 2004b, 2005; Mortensen & Fosså 2006). The associated organisms of coral and sponge reefs are comprised mainly of species that occur on other hard-bottom substrates and their relationship is facultative.

Fig. 1. The composition and sediment types in different marine landscapes on the Norwegian shelf and slope from the coast to the deep sea plain. The depth range of banks in this region is from 50 to 200 m. The shelf break occurs at depths between 200 and 400 m, while the abyssal plain is below 2400 m depth. The figure is based on substrate types observed during MAREANO mapping surveys using video equipment in 2008 (http://www.mareano.no).
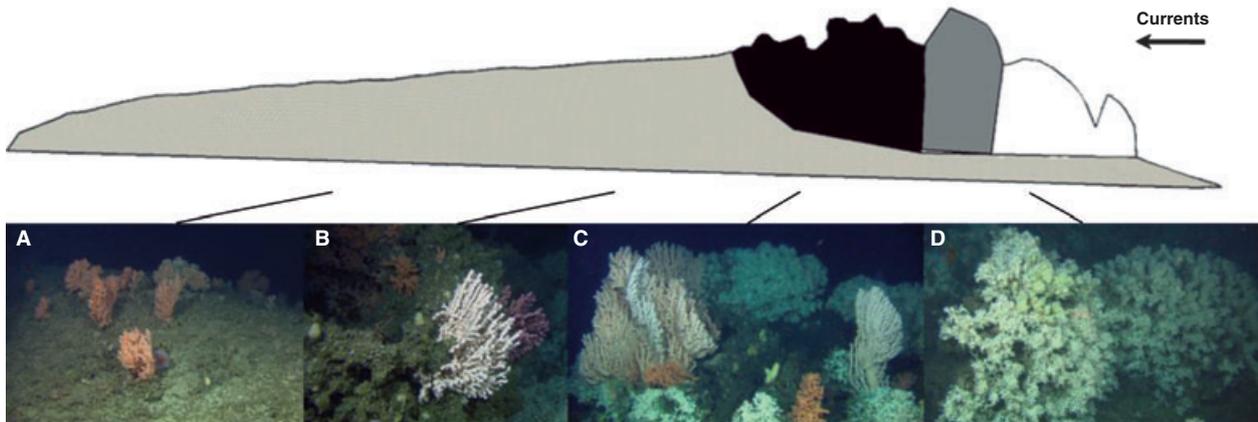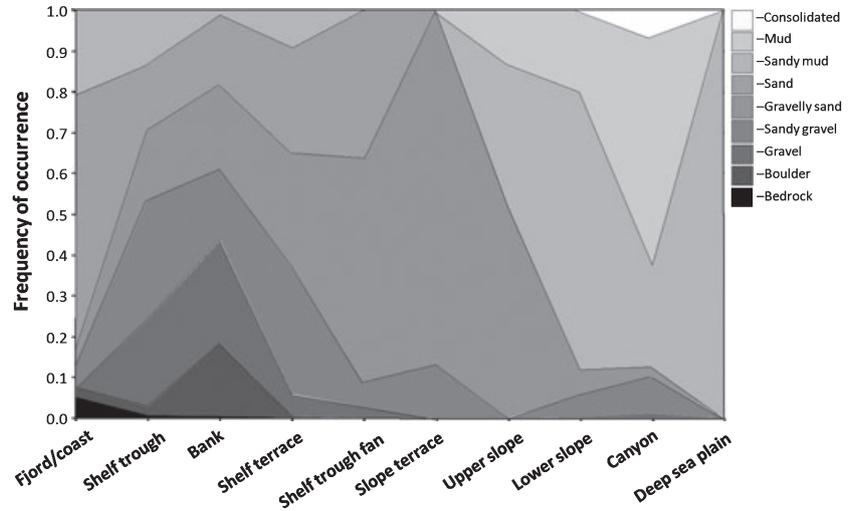
Fig. 2. Zonation of habitats along an elongated *Lophelia* reef off Norway (modified from Mortensen *et al.* 2008b). (A) Reef 'tail' consisting of *Lophelia* rubble, with the gorgonian *Primnoa resedaeformis*. (B) Blocks of dead *Lophelia* colonies with *Paragorgia arborea* and *P. resedaeformis*. (C) Transition zone with recently dead *Lophelia* colonies and gorgonians. (D) The living 'head' of the reef with 'half moon'-shaped colonies facing the main current.

The upper bathyal zone (500–1500 m)

This zone is often heterogeneous due to topographic complexity (MacIlvaine & Ross 1979) and exhibits a greater variability of sediment characteristics than deeper sea beds (Bett 2001; Mortensen *et al.* 2009). In some regions, the margins are intersected by submarine canyons (Rowe 1971; Mortensen *et al.* 2009; Ramirez-Llodra *et al.* 2010; Schlacher *et al.* 2010). While much of the terrain is gently sloping (∼5%) level bottom, with sandy mud and scattered gravel, canyons provide varied topography and substrate heterogeneity. Canyons form distinct habitats and complex current patterns, with coarse, gravelly sediments in the shallow axis and consolidated clay (topographically complex firm substrate) or soft sediments in the deeper parts (Bouma 1965). Complex hydrodynamic patterns caused by topographic features can induce intensified, near-bottom flow in canyons (Shepard *et al.* 1979; Gage *et al.* 1995; Gage 1997) where turbidity currents may also be active (Jorissen *et al.* 1994). In these settings, large, biogenic structures formed by reef-building organisms are found in the upper range (Zibrowius 1980; Rogers 1999; Mortensen *et al.* 2008a), while sea pens and gorgonians are amongst the larger organisms responsible for creating complex biotic habitats (Mortensen *et al.* 2008a).

On the upper slope, internal tides, water column instability, and storm-driven eddies may create strong, erosional currents (Dickson & McCave 1986; Pingree & New 1989; Rice *et al.* 1990; Gage 1997). The currents on the upper slope in the Rockall Trough (<1000 m) frequently have velocities exceeding 15 cm·s^{-1} (Paterson & Lambshead
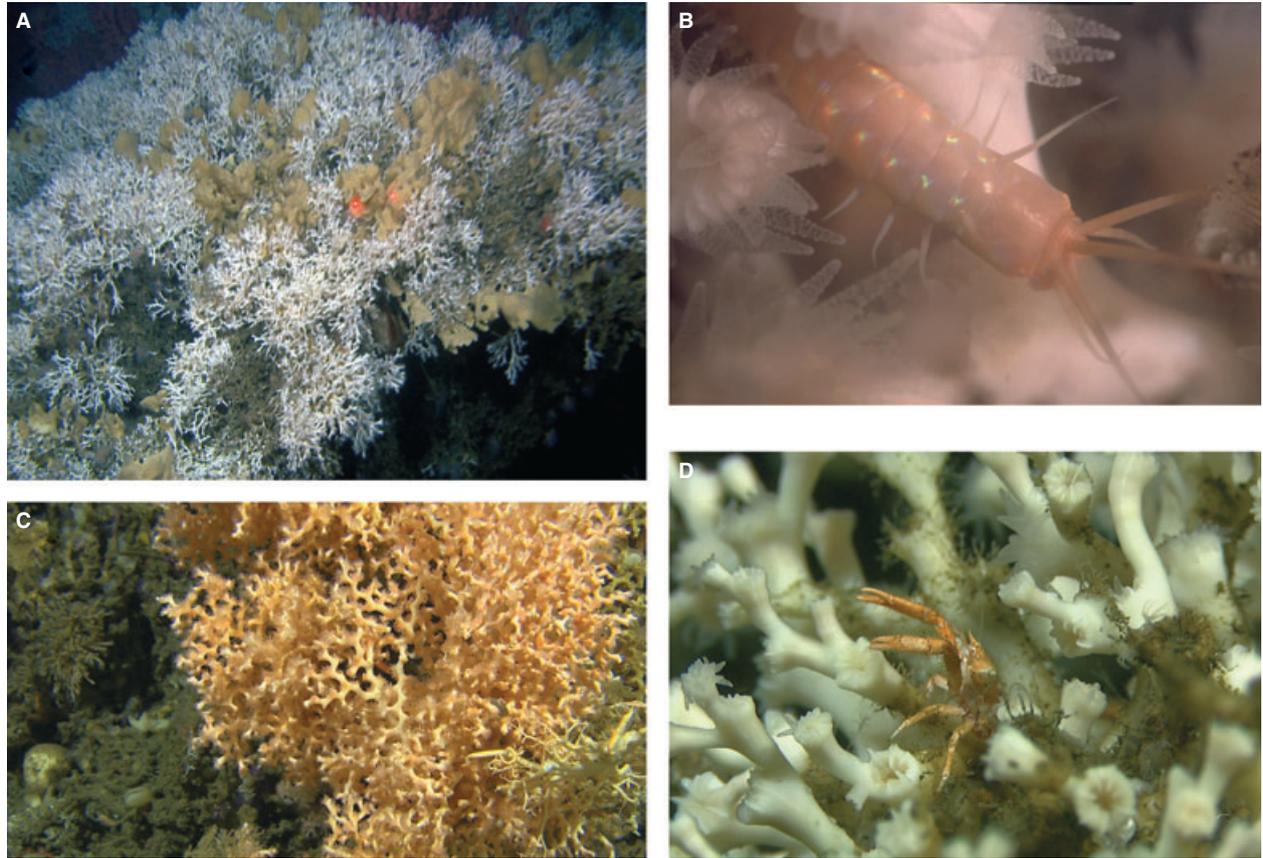
Fig. 3. Pictures of deep-water reef habitats off Norway. (A) Living part of a *Lophelia* reef with sponges. (B) *Eunice norvegica* is a common polychaete living intimately with the polyps of *Lophelia*. It is not obligate on *Lophelia* but rarely occur in other habitats. (C) The scleractinian *Madrepora oculata* with the basket star *Gorgonocephalus* sp. (lower right). (D) The squat lobster *Munidopsis serricornis* on the branches of *Lophelia*.

1995) and peak flows reaching 48 cm·s^{-1} (Viana *et al.* 1998). On the upper slope around the Northwest European continental margin, interactions between the sea floor and internal waves co-occur with conspicuous concentrations of hexactinellid sponges (Rice *et al.* 1990) and corals (Frederiksen *et al.* 1992). Dense, narrow bands of xenophyophores on the Northwest Atlantic margin (Hecker *et al.* 1980) and on the tails of mounds in the Northeast Atlantic (Bett 2001) reflect strong regulation by flow.

The lower slope (1500–2500 m)

The lower slope is less heterogeneous (Bett 2001), but still more varied than the deep-sea plain (>2500 m), where there are vast areas with level, muddy bottoms (Fig. 1). For the deep-sea biota, the decrease with depth in population differentiation (Etter & Rex 1990), species diversity (Rex 1983) and zonation (Grassle *et al.* 1975, 1979; Rex 1977), and the increase in bathymetric and geographic range (Etter & Rex 1990), suggest that the environment is more diverse in the upper bathyal region and becomes progressively more uniform as depth increases. The presence of corals, sea pens, sea lilies and sponges on the deep-sea floor offers rare, firm substrates for sessile organisms in an otherwise featureless environment (Fig. 6). Such biotic structures can thus act as habitat islands in the deep sea. As a result, the relative importance of elevated biotic habitats for local biodiversity may be greater for the deep sea than for shallower bottoms, where coarser sediments are more common.

The deep-sea floor (>2500 m)

The general setting of the deep-sea floor environment is uniform, muddy sediment and low currents with few food particles (Carney 2005); these features limit the occurrence of organisms that require a firm substratum and/or food particles carried by the water current (Beaulieu 2001). Biological structures that reach into the near-bottom boundary layer can provide habitats that are not present in the surrounding areas. Single individuals of corals, glass sponges, sea pens and giant testate protists
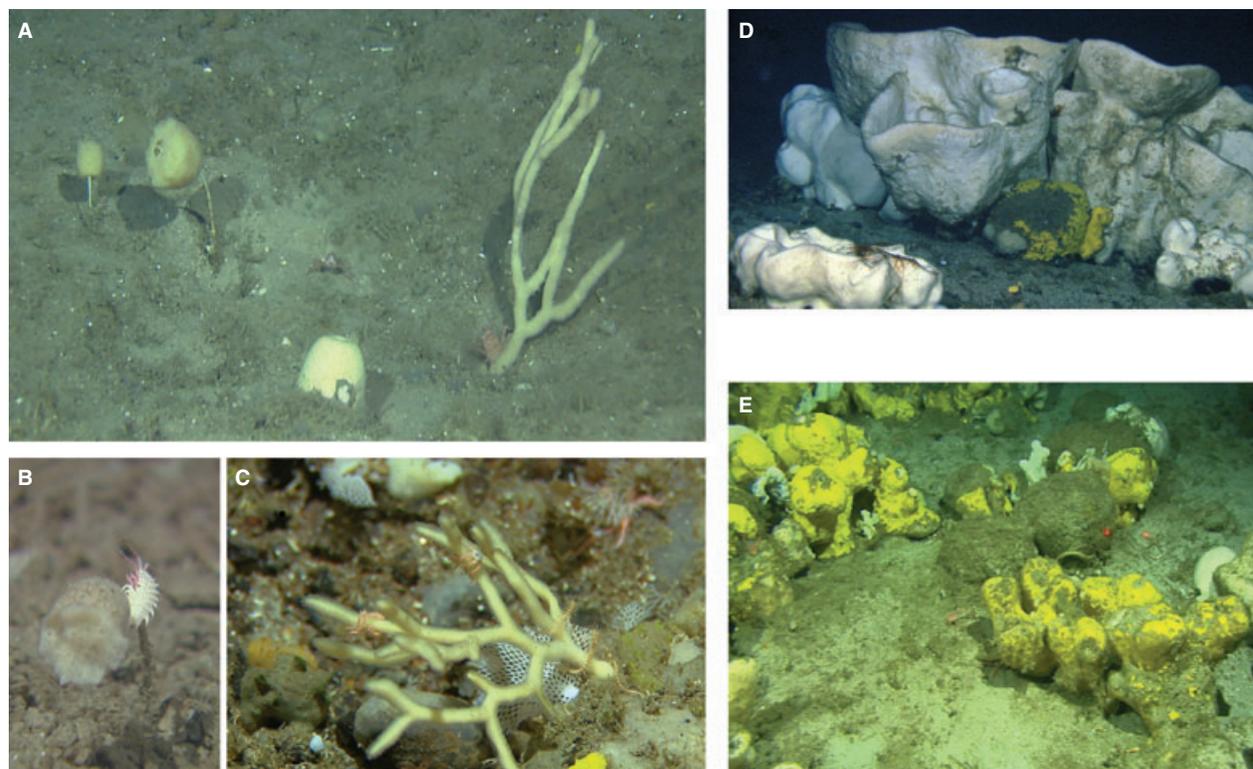
Fig. 4. Examples of different morphology and habitats of sponges (A) *Stylocordyla borealis*, *Antho dichotoma* and an unidentified round sponge. (B) *Stylocordyla* with an associated amphipod. (C) *Antho dichotoma* with an ophiacanthid brittlestar attached to the branches. (D) *Geodia atlantica*. (E) Dense field of *Stryphnus phlegraei* covered with *Aplysilla sulphurea*. Photographs: MAREANO, IMR.

(*e.g.* xenophyophores) can provide a firm substratum and altered food supply for the associated fauna. These organisms will often be colonized by species that are not common in the surrounding habitat, and thus they are considered local hotspots of activity and diversity (Levin 1991; Beaulieu 2001). Often, larvae are available, but substratum is lacking. This is especially evident from studies of fauna attached to cables, shipwrecks, and pipelines brought up from great depth (Duncan 1877, Lampitt 1990, Bell & Smith 1999).

Food supply and the benthic boundary layer

The deep-sea environment is dominated by detritus and resuspension feeders and a gradient of food influx constrains species depth distribution (Smith & Hinga 1983; Levin *et al.* 2001; Carney 2005). The decrease in particulate organic carbon (POC) flux from the shelf to the abyssal plain is well documented for gradually sloping margins (Smith & Hinga 1983; Levin *et al.* 2001; Carney 2005) but becomes more complicated with the irregular slopes intersected by canyons. It is also well established that the influx of detrital food decreases rapidly with depth, while changes in food type are more tentatively identified (Car-

ney 2005). Thus, deep-sea benthic animals must adapt to a food-poor environment. The near-bottom transport of food particles is vital for these organisms and depends on the nature of the benthic boundary layer (BBL).

The BBL is the zone of water and sediment immediately adjacent to the bottom. It represents a strong gradient of energy, dissolved and solid chemical components, suspended matter and the organisms that live there (Boudreau & Jørgensen 2001; Perlin *et al.* 2005). The BBL is not a physically distinct layer, but is defined as the interface between the surface of the solid and an arbitrarily selected distance away from that surface, where the shear effect on flow becomes 'negligible' (Boudreau & Jørgensen 2001). It is subdivided into a very thin 'diffusive boundary layer and a viscous layer' a few millimeters thick, dominated by molecular viscosity and roughness creating turbulence, and a 'logarithmic layer' (Fig. 7). The logarithmic layer involves flows in which the velocity profile is represented by a logarithmic increase away from the bottom substratum.

In deep-sea environments with slow currents and fine sediments, the BBL is narrow, whereas in the high-current environment of shallow waters, the BBL may involve a larger part of the water column (Souza & Friedrich 2005).

Fig. 5. Gorgonian corals occurring in great densities are often referred to as gorgonian forests or coral gardens. They provide wide open three-dimensional complex habitats with colonies ranging up to *c.* 3 m above the bottom. (A) Dense stand of *Paragorgia arborea* mixed with *Primnoa resedaeformis* at 200 m off Norway. (B) Pandalid shrimp and *Gorgonocephalus* sp. (Ophiuroidea) among the branches of *Paragorgia*. (C) Gall formed by the obligate parasitic copepod *Gorgonophilus canadensis* living inside *Paragorgia*.

The general pattern of decreasing BBL thickness and the decreasing amount of food particles available at increasing depths, implies that a slight elevation of even just a few centimeters above the soft-bottom, deep-sea floor into the logarithmic part of the BBL will offer a great change in available food sources. On the shelf and upper slope, the near-bottom gradients of food resources and current will be less pronounced in the broad BBL.

The relative abundance of food at the shelf-slope transition argues against food limitation in this zone and focuses attention upon physical factors (Carney 2005). Internal waves on continental margins can induce resuspension and even an upward transport of particles in periods of strong wind (Bonnin *et al.* 2002). Here, biological structures such as sponges and corals can provide shelter to some organisms, protecting them from strong currents and a 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) (Figs 2 and 8) (Buhl-Mortensen & Mortensen 2004b).

Biotic habitats

On the deep-sea floor, level muddy sediments and low currents with few food particles are characteristic of the general environment. This limits the occurrence of organisms that require a firm substratum and/or food particles carried by water currents (Barthel *et al.* 1991; Beaulieu 2001). Organisms associated with biological structures that provide a firm substratum reaching into the near-bottom boundary layer containing bottom currents will have more food particles and other resources available to them than will be present in 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 (Fig. 8) represent a scarce habitat, contributing substantially to the species richness of their respective environments (Beaulieu 2001; Buhl-Mortensen & Mortensen 2004b). Structures such as tubes, skeletons, tests or stalks of epibenthic organisms protrude from the sea floor, providing a hard substratum that elevates suspension feeders into the BBL flow (Barthel *et al.* 1991; Levin 1991; Gooday *et al.* 1992). These organisms will commonly offer internal space, crevices and increased surface area for colonisation, with larger individuals creating more habitat. The relationship between fish and large, habitat-forming species (*e.g.* corals and sponges) will be treated separately. Many large epibenthic species are long-lived (Freiwald *et al.* 2002; Mortensen & Buhl-Mortensen 2005) and generate substrates of different ages which allows for simultaneous occurrence of epibiotic communities in different states of succession (*e.g.* Grassle & Morse-Porteous 1987).
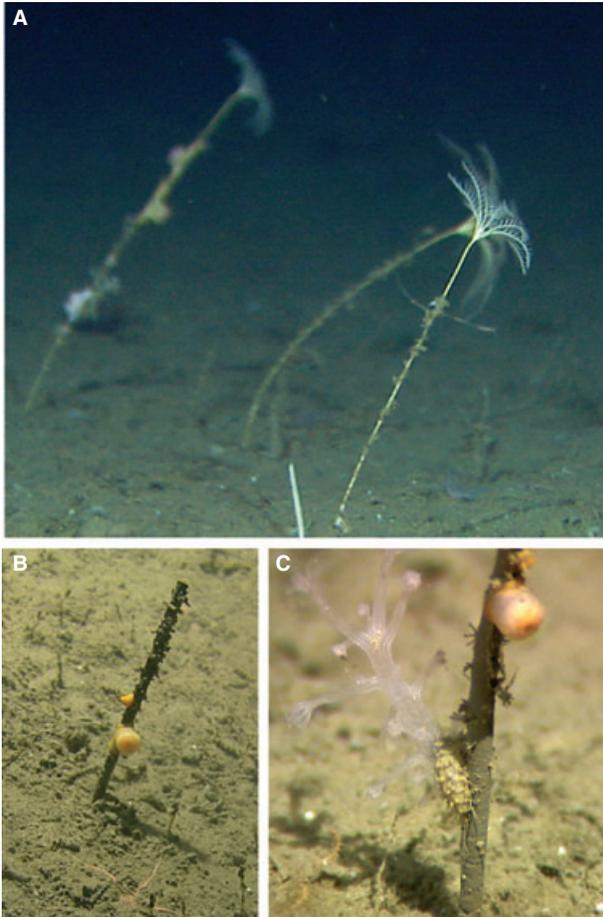
Fig. 6. Organisms in the deep sea that provide firm substrates reaching into faster-moving water above the bottom in the benthic boundary layer. (A) Sea lilies, *Rhizocrinus lofotensis* providing substrate for anemones, colonies of nestbuilding amphipods and hydroids. (B) Sabellid polychaete tube with amphipod nests and anemones. (C) Sabellid polychaete tube with nephtheid coral, scale worm (Polynoida) and anemone.
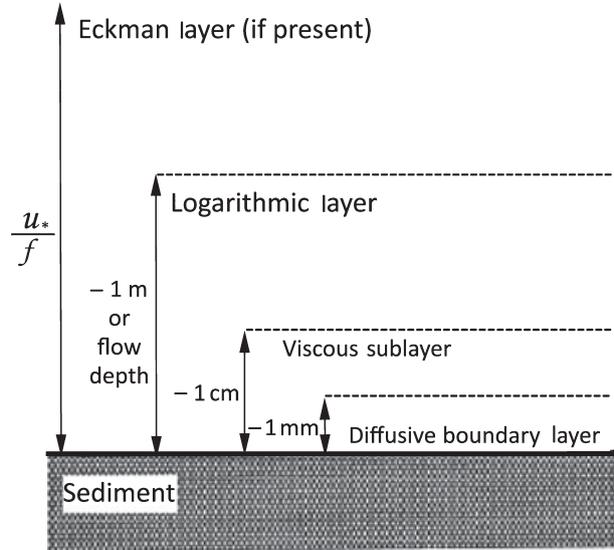
Fig. 7. The Benthic Boundary Layer (BBL) is subdivided into a 'bed layer' a few millimeters thick, dominated by molecular viscosity and roughness creating turbulence, and a 'logarithmic layer'. The Logarithmic layer involves flows in which the velocity profile is represented by a logarithmic increase away from the bottom substratum (Boudreau & Jørgensen 2001).

Habitat heterogeneity can be measured at several scales by using different physical variables or indices (*e.g.* broad scale-variation in topography and sediment and local variation in surface: volume ratios for single biotic habitats). The community of biotic substrates is a function of the physical and chemical environments and the interactions between species. Some of these interactions represent co-evolution driven by predator–prey interactions or by the mutual benefits between symbionts and their hosts.

At a local scale, the morphology of organisms shapes the environment by modifying the hydrodynamics, and pro-
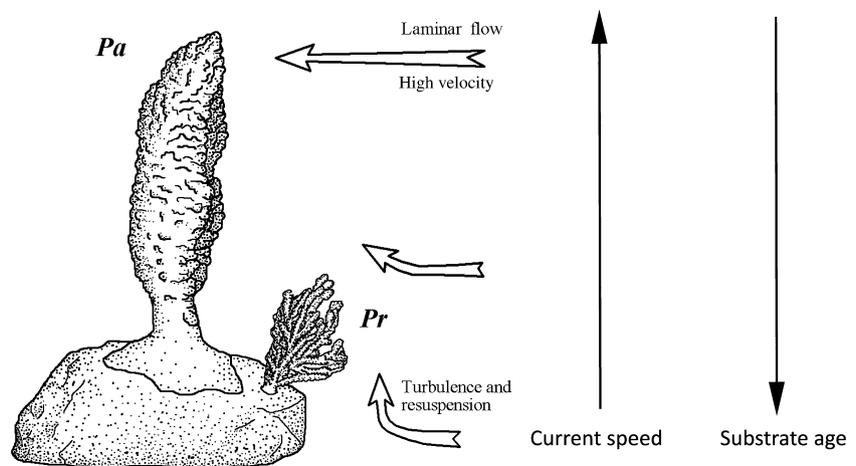
Fig. 8. Morphological adaptation to local current patterns illustrated with the gorgonian coral *Paragorgia arborea* (Pa) and *Primnoa resedaeformis* (Pr) (Mortensen & Buhl-Mortensen 2005).

Table 1. Overview of microhabitats provided by major biotic habitat-forming taxa and water masses where they mainly occur. X: most common. x: less common.

habitat	Protista		Porifera		Octocorallia			Scleractinia	
	Xeno	Hexact	Demo	Calc	Penna	Alcyo	Gorgon	Soli	Col
live tissue									
inside						x	x	x	x
outside	x	x	X	x	x	x	X	x	x
exposed skeleton									
inside									
outside	x	X							X
sheltered space									
cavities	x	x	x	x					X
canals	x		X						
water mass (depth)									
shallow		x	x	X	x	x	x	x	x
intermediate	x	x	X	x	X	X	X	X	X
deep	x	X	x	x	x	X	x	X	x

Xeno = Xenophyophorea; Hexact = Hexactinellida; Demo = Demospongia; Calc = Calcarea; Penna = Pennatulacea; Alcyo = Alcyonaria; Gorgon = Gorgonacea; Soli = solitary; Col = colonial.

Table 2. Overview of habitat aspects (size, substrate flexibility and 3-D complexity) of major biotic habitat-forming taxa.

	size		
	small (<25 cm)	medium (25–300 cm)	large (>3 m)
substrate flexibility			
rigid	Solitary scleractinians Xenophyophorea (some)	Colonial Scleractinia	Reef-forming scleractinians
flexible	Porifera, Gorgonacea, Antipatharia, Pennatulacea Xenophyophorea	Porifera, Gorgonacea, Antipatharia, Pennatulacea	Reef-forming sponges
soft	Porifera, Alcyonaria, Xenophyophorea	Porifera, Alcyonaria	
complexity (surface/volume)			
low	Sponges, Gorgonacea	Sponges, Gorgonacea	
medium	Solitary scleractinians	Sponges, Pennatulacea, Gorgonacea	
high	Xenophyophorea	Colonial Scleractinia	Reef-forming scleractinians

viding shelter, pockets with trapped particles, and other microhabitats (Table 1). Such local environmental conditions are extremely difficult to study *in situ* within 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 (Table 2).

Corals

Cold-water corals are found around the world, most commonly in the depth range of 200–1500 m (Broch 1912, 1935, 1957; Jungersen 1917; Madsen 1944; Carlgren 1945; Hecker *et al.* 1980; Zibrowius 1980; Genin *et al.* 1986; Tendal 1992; Cairns 1994; Rogers 1999; Mortensen *et al.* 2006). Very shallow, upper depth limits (up to 40 m) of cold-water corals in Norway, New Zealand, Chile and British Columbia demonstrate that it is not the depth *per se*, but the distribution of intermediate and deep water masses that controls the bathymetric distribution of these corals

Corals typically create habitats reaching from decimeters to meters above the surrounding seabed and occur on mixed bottoms in areas with relatively high currents. They offer a variety of microhabitats with different current speeds, food sources and substrates (Table 3). Most corals have an arborescent morphology with branches elevated into faster flowing water above the relatively still near-bottom boundary layer closer to the bottom. Corals have a complex architecture, and provide substrata of different

Table 3. Habitats and resources provided by major biotic habitat-forming taxa.

biotic habitat	Available habitat			Resource for associates				
	on	among	within	current	substratum	detritus trapped	predator protection	food
Lophelia								
live		x		x			x	
dead	x	x	x	x	x	x	x	
rubble	x		x		x	x		
sand								
gorgonians								
live	x	x	x	x			x	x
dead	x		x			x		
seapens	x		x	x	x		x	x
glass sponges	x		x	x				
Demospongia	–	x	x		–	x		x
Xenophyophorea	x		x		x	x	x	x

age. Sheltered cavities within a colony often contain organic-rich sediments, while the outer parts provide a high water flow with little sedimentation.

Gorgonian corals

Structural attributes. Gorgonian corals provide habitats within colonies and between colonies, when they occur in stands. The density of colonies within stands is typically higher for smaller species than for larger species (Mortensen & Buhl-Mortensen 2004). This is illustrated by results from the Northeast Channel, Nova Scotia, where Mortensen & Buhl-Mortensen (2004) found maximum densities of 199 colonies per 100 m^2 for the small gorgonian *Acanthogorgia armata*, whereas the large *Paragorgia arborea* occurred with a maximum of 49 colonies per 100 m^2. The gorgonian stands vary in horizontal extent from 10 to 100 m (Mortensen & Buhl-Mortensen 2004).

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. In addition to accessing faster-flowing water above the bottom, colonies orient to maximise the amount of water passing the polyps (Wainwright & Dillon 1969). The advantages of morphologically enhanced feeding by the gorgonians are also passed on to any rheophilic, filter-feeding, epizoic animal associated with the colony. In addition, filter-feeding organisms may also derive nutrition from detritus or microorganisms commonly found trapped in the mucus secreted from the gorgonian colonies (Patton 1972). *Primnoa resedaeformis* and *Paragorgia arborea* are the most abundant and widely distributed large gorgonians in the North Atlantic (Madsen 1944; Tendal 1992; Mortensen & Buhl-Mortensen 2004; Mortensen *et al.* 2006), where they can form

'coral gardens' or thickets (Fig. 5). They are amongst the largest deep-sea gorgonian corals, reaching heights of 50–250 cm.

The deep-water gorgonians offer two different micro-habitats 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 (Table 4).

Associated fauna. The gorgonian-associated fauna is dominated by crustaceans, particularly amphipods. This is true for tropical gorgonians (Goh *et al.* 1999), which also host parasitic copepods, but deep-water gorgonian taxa exhibit a richer echinoderm fauna, including ophiuroids adapted to capturing particles in the elevated flows provided by the corals (Emson & Woodley 1987; Fujita & Ohta 1988). The deep-sea gorgonians have fewer decapods (crabs and shrimps) and gastropods than warm-water corals (Patton 1976; Goh *et al.* 1999). In a study focusing on the associated fauna of deep-water gorgonians, Buhl-Mortensen & Mortensen (2005) found that only a few specialised and obligate symbionts are connected to the live parts of corals (Figs 3 and 5). Among these are three species of highly specialised parasitic copepods, presumed to feed on the coenenchyme of their hosts (Patton 1976). However, the number of obligate symbionts is higher for gorgonians than for antipatharians, alcyonarians and scleractinians. Buhl-Mortensen & Mortensen (2005) found that 24 species are reported as being in obligate relationships with 21 host species (Appendix 1). For comparison, the literature reports only four scleractinian species and higher taxa with a total of seven obligate symbionts.

The corals *Paragorgia arborea* and *Primnoa resedaeformis* host a rich fauna, dominated by suspension feeders using the coral as substratum or refuge against predators

Table 4. Relation between associated taxa and host coral for habitat 1 (young parts of the colony) and 2 (old parts) of *Paragorgia arborea* and *Primnoa resedaeformis*.

habitat	refuge	feeding site	food
Paragorgia			
1. young sections	*Pandalus*	*Gorgonocephalus*	Parasitic copepods
		Pandalus	Polynoid polychaetes
		Anemones	Anemones
2. old sections	*Pandalus*	Hydroids	Polynoid polychaetes
	Amphipods	Foraminifers	
	Ostracods	Amphipods	
	Polychaetes	Polychaetes	
		Ornatoscalpellum	
Primnoa			
1. young sections	*Pandalus*	*Pandalus*	Parasitic copepods
			Acarina
2. old sections	*Pandalus*	*Pandalus*	*Epizoanthus* sp.
	Amphipods	*Ornatoscalpellum*	
	Isopoda	Hydroida	
	Ostracoda	Amphipods	
		Foraminifers	
		Epizoanthus sp.	
		Bivalves	
		Balanids	

Table 5. The correlation coefficients (r) between abundance (N), species richness (S) and diversity (H′) of associated fauna of *Paragorgia arborea* and *Primnoa resedaeformis* and seven measurements of host morphology.

coral measurements	*Paragorgia*			*Primnoa*		
	N	S	H′	N	S	H′
wet weight (g)	−0.02	0.62**	0.53*	0.26	0.19	0.35
width of fragment/colony (cm)	0.19	0.32	0.31	0.42	0.3	0.46
length of fragment/colony (cm)	0.34	0.28	0.35	0.48	0.37	0.54*
no. branches (>3 cm)	0.11	0.66**	0.51*	0.43	0.28	0.44
base width (cm)	0.07	0.48*	0.4	0.27	0.26	0.41
% exposed skeleton	–	–	–	0.54*	0.5	0.56*
no. of rings in base	–	–	–	0.39	0.3	0.48

*$P < 0.1$, **$P < 0.05$ (data from Klitgaard 1995).

(Table 4) (Buhl-Mortensen & Mortensen 2004b,c, 2005). The faunal composition differs for the two gorgonians but consists mainly of species also occurring in other habitats. However, Buhl-Mortensen & Mortensen (2004b,c, 2005) identified a few highly specialised parasites associated with each of the species. The abundance and diversity of the associated fauna are significantly correlated with host morphology (*i.e.* number of branches and area of exposed skeleton) (Table 5). The species richness of the deep-sea gorgonian coral fauna is higher than that of tropical gorgonians, but the deep-sea forms support fewer obligate associations (Table 6). Nevertheless, several of the associated species are rare in other habitats and seem to have a preference for one or more gorgonian species (Buhl-Mortensen & Mortensen 2004a).

Reef-forming scleractinians
Structural attributes. 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 new hard substrate for subsequent colonisation. Colonies that have grown at one site for hundreds of years transform the bottom to a cover of coral skeleton fragments via alternating growth, death and fragmentation. The area can then be termed a coral reef. 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 (Mortensen *et al.* 2001). Many of these reefs are several 100 m long, and occur in clusters (reef complexes) up to 35 km long (Røst reef) (Fosså *et al.* 2005). Their surfaces, however, cover

Table 6. Comparison between shallow- and deep-water corals of the percentage composition of symbiotic species belonging to different taxa.

	shallow (obl.)	deep (obl.)	deep (fac.)	deep (unknown)
Protozoa				
Foraminifera	0	0	2	0
Porifera	1	0	0	0
Cnidaria	3	3	4	1
Polychaeta	5	11	8	4
Arthropoda				
Pycnogonida	0	0	1	0
Cirripedia	5	14	5	10
Copepoda	34	2	1	1
Tanaidacea	0	0	1	0
Amphipoda	1	0	7	1
Isopoda	0	0	3	0
Decapoda	29	2	12	0
Mollusca				
Gastropoda	15	2	2	0
Bivalvia	5	0	3	0
Echinodermata				
Ophiuroidea	2	2	10	0
Asteroidea	0	0	2	0
no. of species	311	36	61	17

obl. = obligate symbionts. fac. = facultative symbionts. unknown = unknown status. (from Buhl-Mortensen & Mortensen 2004a).

<0.1‰ of the total area in the depth zones where they occur. They commonly display vertical zones, with living coral at the top and skeletal fragments at increasing stages of decay towards the bottom of the reef (Mortensen *et al.* 1995) (Fig. 2). Three successive habitats can be observed when crossing a reef: the coral rubble zone consisting of small pieces of skeleton, followed by the coral block zone dominated by large blocks of coral skeleton, which lead to the live coral reef. Four different microhabitats can be recognised within the coral colonies of the live reef: (i) tissue of living corals, (ii) detritus-laden surfaces of dead corals, (iii) cavities inside coral skeletons, and (iv) free space between coral branches.

As many similar microhabitats can be found on bottoms without corals, the majority of coral-associated species are facultative symbionts without a direct relationship to the living corals (Mortensen & Fosså 2006). 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 (Mortensen & Fosså 2006 and references therein).

Faunal associates
Macrofauna. The diversity of animals found together with cold-water, reef-forming corals is high (Reed *et al.*

1982; Reed & Mikkelsen 1987; Jensen & Frederiksen 1992; Rogers 1999; Mortensen & Fosså 2006), although there are no examples of obligate relationships between associated species and dead coral skeleton. The live tissue of deep-water scleractinian corals seems to prevent attachment of sessile epibiotic species. Even among the few species commonly found intimately associated with living coral polyps, there are few, if any, examples of obligate relationships (Buhl-Mortensen & Mortensen 2004a). However, many of these species are seldom found in other habitats. The polychaetes *Eunice norvegica* and *Harmothoe oculinarum* are two good examples of this. *Eunice norvegica* lives in a close relationship with *Lophelia pertusa*. The coral precipitates calcium carbonate around the parchment-like tube of the polychaete. After years of skeletal growth, *E. norvegica* has a tube with several openings, each close to a polyp, where it can look for food spills (Mortensen 2001). *Eunice norvegica* spends time searching for food and removing organic particles from the surface of the coral. It also removes organisms invading or colonising its territory (Mortensen 2001). This allows easy access to food trapped by *L. pertusa*. The polynoid polychaete *H. oculinarum* lives as a commensal inside the tube of *E. norvegica*. The highest diversity of associated species is found in the zone with dead coral blocks (Table 7) (Jensen & Frederiksen 1992; Mortensen & Fosså 2006). Here, the skeletons are exposed and occur with a higher three-dimensional complexity than in the rubble zone surrounding the reefs.

Meiofauna of the coral rubble zone. On a small spatial scale, the presence of coral rubble and associated microhabitats at the ocean margins greatly influences the meiobenthic community living in close association with *Lophelia* reefs. These communities have been studied in detail within the Belgica Mound area of the Porcupine Seabight (Northeast Atlantic) (Raes & Vanreusel 2005, 2006; Gheerardyn *et al.* 2009a,b), although information on the meiofauna in other cold-water coral environments is still lacking or is very limited (Jensen & Frederiksen 1992).

Coral rubble provides a coarse substrate that hosts specific faunal taxa and lifestyles. Compared to their underlying sediment environments, dead *Lophelia* and *Aphrocallistes* skeletons were characterised by significantly lower nematode densities and higher densities of other taxa such as harpacticoid copepods (Table 8) (Raes & Vanreusel 2005). Furthermore, the nematode communities on coral fragments are significantly different, both at the genus and species levels, from those in the underlying sediment (Table 9) (Raes & Vanreusel 2006). The nematofauna in the sediment is dominated by fine and slender species, typical of the slope sediment-inhabiting genera (*e.g. Sabatieria*, *Acantholaimus*) that move with a 'nor-

Table 7. Total weight (g), volume (ml), abundance and diversity of associated macrofauna of *Lophelia pertusa* coral skeleton in four categories with respect to the proportion of dead skeleton. The habitat abbreviations are the same as in Table 2. The LL habitat is divided into two categories, one with a low percentage live coral (1–20%), and one with high percentage live coral (>20%). The percentage of live coral is based on skeleton weight. Standard deviation is in parentheses. (Mortensen & Fosså 2006).

habitat	LR	DL	LL (1–20%)	LL (>20%)
no. of samples	4	7	7	6
weight of coral	1042 (163)	5206 (556)	12263 (2192)	2089 (334)
% live coral	0	0	14.3 (5.4)	55.7 (28.5)
% open volume	57 (3.9)	60 (7.3)	57 (6.9)	73 (10.7)
Individuals and colonies per 100 g coral	94.9 (56.4)	65.9 (84.5)	66.2 (86.9)	145.3 (100.0)
mean diversity (H')	3.8 (0.9)	4.3 (1.0)	4.8 (0.5)	4.0 (0.6)
species per 100 g coral	16.6 (10.9)	7.8 (4.7)	12.5 (17.8)	38.0 (39.3)
total no. of species	107	186	255	151

biogenic habitat	relative abundance (%)				
	Nematoda	Harpacticoida	Nauplii	Polychaeta	others
dead *Lophelia*	58.6	17.9	8.7	8.1	6.7
skeletons of *Aphrocallistes*	77.2	10.6	1.6	6.1	4.5
mixed substrate (coral fragments and sponge skeletons)	78.9	8.3	1.4	4.9	6.5
underlying sediment	85.8	5.5	2.5	3.0	3.2

Table 8. Relative abundances of the meiofauna associated with the cold-water coral degradation zone, for each microhabitat distinguished.

Genus	underlying sediment (%)	mixed substratum (%)	coral fragments (%)	sponge skeletons (%)
Acantholaimus	6.78	4.88	6.70	4.61
Actinonema	1.28	2.11	2.77	6.15
Calomicrolaimus	2.15	1.04	2.34	4.75
Ceramonema	2.85	4.96	1.64	5.19
Desmodora	5.68	2.37	1.39	2.67
Desmoscolex	9.01	9.66	7.71	7.85
Epsilonema	0.29	3.23	8.51	0.78
Halalaimus	4.10	4.62	6.84	6.59
Pselionema	1.28	6.06	1.33	7.56
Sabatieria	8.27	2.81	1.33	2.37

Table 9. Nematode genera (with a relative abundance of minimum 5% in at least one microhabitat) from the cold-water coral degradation zone, per microhabitat.

mal', undulating locomotion. The coral fragments reveal much higher abundances of taxa that are better able to cope with current-driven disturbance by (i) their attachment to the substrata, (ii) a specially adapted mode of locomotion and/or (iii) a heavily cuticularised body. Nematodes belonging to the closely related families Epsilonematidae (Fig. 9) and Draconematidae are characterised by unique locomotory structures that enable them to attach themselves onto and/or crawl over a certain substratum just like a geometrid caterpillar (Stauffer 1924; Lorenzen 1973). *Epsilonema* (Epsilonematidae) dominate the nematode communities on coral fragments

and several representatives of both families are recognised as indicator genera for this microhabitat. Other taxa, such as *Desmoscolex* and representatives of the family Ceramonematidae, which have a strengthened cuticle as well, are also abundant on coral fragments and sponge skeletons, respectively. Coral fragments are dominated by epistratum feeders, probably due to the presence of a microbial biofilm covering the coral surface (Freiwald & Wilson 1998), which provides a potential food source.

The harpacticoid copepod fauna associated with cold-water coral degradation zones is characterised by a family composition similar to those reported in other studies of

Fig. 10. *Lobopleura expansa* (Sars, 1908), a member of the harpacticoid family Ancorabolidae Sars, 1909 with a strongly dorsoventrally flattened body shape. Several specimens were collected from a dead fragment of *Lophelia pertusa*.

Alcyonarian corals

The alcyonarian corals (soft corals) utilise a wide range of substrates, including semi-consolidated mudstone. Alcyonarian corals, in particular Nephtheidae, have a wide geographical and bathymetric distribution (Mortensen *et al.* 2006, 2008). The colonies are rather small (<30 cm), but may occur in relatively high densities (>500 colonies per 100 m^2) (Mortensen *et al.* 2006). 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 (Fedotov 1924; Mortensen 1927; Hendler 1991). Mortensen (1927) observed juveniles of the basket star, *Gorgonocephalus eucnemis,* parasitic on *Eunephtia*, and Fedotov (1924) 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 (Buhl-Mortensen & Mortensen 2004a). Compared to the rigid structures of scleractinians and gorgonians, the soft coral represents an unstable substrate not suitable for attached species.

Sea pens

Sea pens reach 0.1–2 m above the sediment surface and access higher bottom currents. They provide shelter

Fig. 9. *Epsilonema multispiralum* Raes, Vanreusel & Decraemer, 2003, a representative of the epifaunal nematode family Epsilonematidae Steiner, 1927. Note the ambulatory setae on the ventral side of the posterior body region.

soft slope and abyssal sediments (Gheerardyn *et al.* 2009a). At the genus and species level, it appears that coral fragments and the underlying sediment does not harbour distinctly different harpacticoid assemblages (Table 10) (Gheerardyn *et al.* 2009b). However, the presence of typically epifaunal taxa indicates that the hard substrates in the coral degradation zone provide a very different habitat than the soft-bottom deep sea. Copepods show distinct morphological specializations as adaptations to the specific conditions of the various habitats (Noodt 1971). Several taxa of the coral degradation zone have a body shape adapted to live as epifauna [*e.g. Lobopleura* (dorso-ventrally depressed; Fig. 10), *Idyanthe* (fusiform depressed), *Tegastes* (laterally compressed)] and some of the identified species (*e.g. Klieosoma triarticulatum, Mesochra pygmaea, Laophonte elongata*) have been reported from the washings of macroalgae (Lang 1948; Hicks & Schriever 1985).

Table 10. Harpacticoid copepod genera (with a relative abundance of minimum 5% in at least one microhabitat) from the cold-water coral degradation zone, per microhabitat.

Genus	underlying sediment (%)	coral fragments (%)	sponge skeletons (%)
Ameira	3.01	8.22	11.61
Halophytophilus	7.52	5.24	2.58
Microsetella	0.75	0.87	6.45
Pseudobradya	3.76	8.04	0.65
Pseudomesochra	9.02	8.22	30.97
Sigmatidium	6.02	9.97	5.81

against predation and elevated position for particle collection away from the slower current in the near-bottom boundary layer (Fig. 8). Sea pens appear to have few associated organisms, although the number of studies is limited. One example of a close relationship is between *Funiculina quadrangularis* and the ophiuroid *Asteronyx loveni,* which is reported from the west coast of Scotland (Hughes 1998) and off northern Norway (MAREANO unpublished data, see Fig. 11). The ophiuroid's elevated position probably enhances access to food particles from the passing water current. It may also benefit from cleaning mucus off the surface of the sea pen. This feeding strategy possibly keeps the coral clean and healthy, just as the snake star, *Astrobrachion constrictum,* does for the antipatharian black coral, *Antipathes fiordensis* (Stewart 1998). Predators on sea pens include nudibranchs, which have been observed preying on sea pen polyps. Shrimps are frequently seen climbing on *Pennatula* on video records of the shelf off Norway (unpublished observations-MAREANO) (Fig. 11).

The nudibranch *Armina loveni* is a specialist predator on the sea pen *Virgularia mirabilis.* This sea slug is infrequently recorded, but is known to occur from Norway to Western France. In Puget Sound, a related species, *Armina californica,* is one of the predators on *Ptilosarcus guerneyi* (Birkeland 1974). Amphipod crustaceans of the family Stegocephalidae also appear to feed on sea pens, but little is known of their ecology (Moore & Rainbow 1984). Many specimens of *Virgularia mirabilis* lack the uppermost part of the colony, a feature that has been attributed to nibbling by fish. Mackie (1987) found that extracts of *Pennatula phosphorea* inhibited feeding in sole *Solea solea,* suggesting that this sea pen may possibly have a chemical defence against fish predation. Shrimp have often been observed on *Pennatula* (MAREANO unpublished results, see Fig. 11). Anemones have been frequently observed at the top of sea pens off Nova Scotia (unpublished results).

Sponges

Sponge attributes. The phylum Porifera consists of three classes: the Hexactinellida (glass sponges), Calcarea (calcareous sponges), and Demospongiae (demosponges), with the last group containing the majority of extant species. Due to the high diversity and large biomass of sponges, and a complex physiology and chemistry, sponges play a key role in a host of ecological processes: space competition, habitat provision, predation, chemical defence, primary production, nutrient cycling, nitrification, food chains, bioerosion, mineralisation, and cementation (Rützler 2004). Sponges create a complex living space for large numbers of species from many taxa. Live sponges can provide hard substratum in an open sediment situation, refuge from predation or physical hazard, and an enhanced food supply (Wulff 2006; Taylor *et al.* 2007). Most species associated with sponge hosts live inside the canals and feed on plankton or particles not used by the sponge or, in some cases, they eat the sponge itself. Sponge structure is homogeneous, malleable
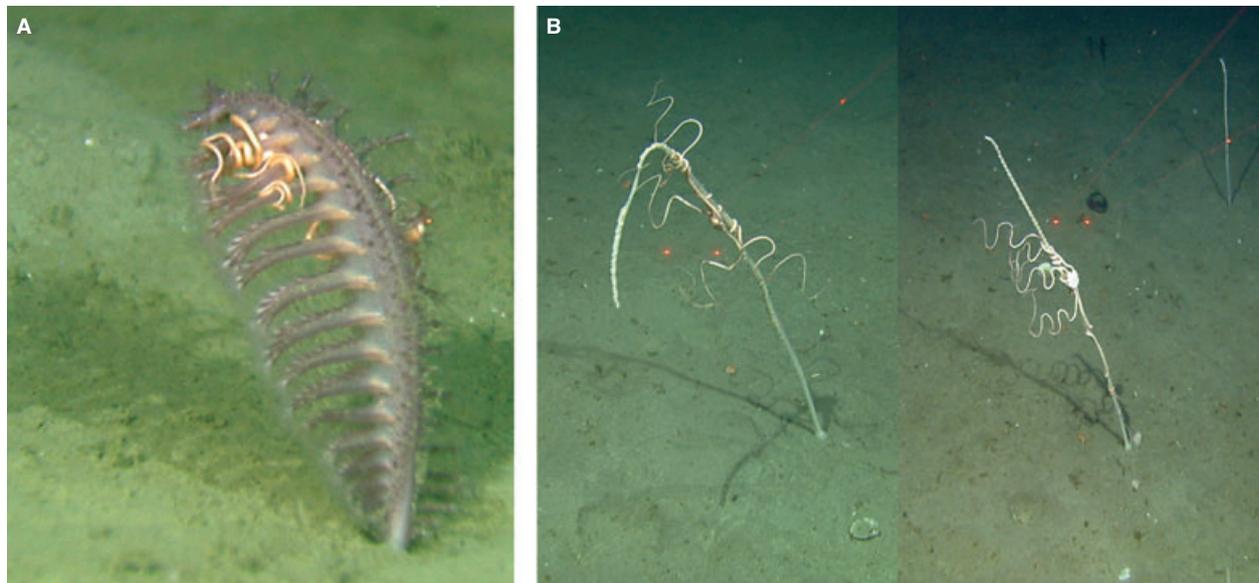
Fig. 11. Sea pens with associated fauna in a framing habitat of sandy mud. (A) *Pennatula phosphorea* with *Asteronyx loveni* and a pandalid shrimp. (B) *Funiculina quadrangularis* with *Asteronyx loveni. Asteronyx loveni* is obligate to sea pens. Photographs: MAREANO, IMR.

and simple, but is pervaded by many canals, and it is believed that this specific organisational structure is what facilitates the development of intimate associations with other organisms. Sponge-associated endofauna exhibit a positive correlation between canal volume and total mass (Rützler 1976), and also between faunal abundance and mean canal diameter (Koukouras *et al.* 1996). Spicules from dead sponges can provide substratum for other organisms (Bett & Rice 1992). Ilan *et al.* (1994) suggested that in deep-water, soft-bottom environments, sponges are porous, hard-substrate microhabitat islands, providing associated fauna with shelter, and possibly also a continuous flow of water with suspended matter. Wulff (2006) lists the following benefits offered by sponges to associates: (i) protection from boring organisms by covering the host (*e.g.* scleractinian corals, bivalves), (ii) protection from predation by coating surfaces (*e.g.* octocorals, bivalves and other sponges), (iii) protection from predators by providing shelter (*e.g.* juvenile spiny lobster, small crustaceans, ophiuroids, scyphozoans, zoanthids), and (iv) provision of food (polychaetes, snapping shrimps, copepods, isopods, amphipods).

Sponge associates. The associations between sponges and other organisms have been recently reviewed, including sponge-associated microorganisms, symbiotic associations, spatial competition, sponges as microhabitats and sponges as a food source (Wulff 2006; Taylor *et al.* 2007). The sponge associates represent facultative commensals that also live in other sheltered habitats, predators and obligate specialists on particular sponge species. Sponge associates appear to be more diverse and ubiquitous in tropical waters than in deep waters. Sponges commonly serve as a dwelling place for associated invertebrates, but some copepod, amphipod, isopods and alpheid shrimps consume their host sponges (Wulff 2006). Molluscs and echinoderms are important spongivores at all latitudes, but significant sponge feeding by vertebrates is a feature of tropical systems only (Wulff 2006).

Hexactinellid sponges

Hexactinellid (glass) sponges with silica-based skeletons are common at abyssal depths and also occur near methane seeps. The silicious spicules remain relatively intact and thus form a habitat for species long after sponge death, in the form of large mounds, individual stalks or spicule mats. They also occur at relatively shallow depths in the Northeast Pacific, off Canada (Conway *et al.* 2005). Here, at depths of 90–300 m, the hexactinellid species *Aphrocallistes vastus* and *Heterochone calyx* form vast reefs covering up to 700 km^2 (Cook 2005). Reefs form in linear patterns along ridges and the rubble associated with living and dead sponges forms mounds that may be up to 14 m high (Conway *et al.* 2005). These sponge reefs support a large number

of species. Among the most ubiquitous megafauna are spot prawns (*Pandalus platyceros*), squat lobsters (*Munida quadrispina*), blood stars (*Henricia* sp.) and ratfish (*Hydrolagus colliei*). These are all common species in British Columbia's subtidal coastal waters. Most significant may be use of the reefs by multiple *Sebastes* spp. (rockfishes) as nursery grounds (Cook *et al.* 2008). Unfortunately, many of these reefs are highly susceptible to damage by fishermen and show signs of trawl damage (Cook *et al.* 2008).

At an abyssal station in the Northeast Pacific (Sta. M 4100 m), the most conspicuous and dense assemblages of suspension feeders are attached to the stalks of hexactinellid sponges in the genus *Hyalonema* (Beaulieu 2001). The stalks, which occur at densities of 0.13·m^{-2}, are the basal columns of spicules that support the sponge bodies tens of centimeters above the sea floor. In a study of photographs of 2418 *Hyalonema* spp. stalks, >8500 individuals were documented. Of these counted suspension feeders, 5581 were foraminifera. The remainder were polychaetes (76%), peracarids (10%) and molluscs (1%). In 35 sampled stalks, there were 144 taxa, with an average of 4.1 taxa per stalk. In addition to the importance of the primary substratum area in determining the number of taxa found on a stalk, secondary substrates were provided by the attached organisms. These associates both increased three-dimensionality, allowing for cryptic fauna, and provide attachment surfaces.

At 1000–1300 m depth off Ireland, dense concentrations (1.5·m^{-2}) of *Pheronema carpenteri* are associated with increased biomass of megabenthos (Bett & Rice 1992). Sponge spicule mats covered about one third of the sea floor in the sponge zone. The spicules provide a suitable substrate for a variety of demosponge species otherwise unable to colonise open sediment. Polychaete abundance was correlated with areas of sponge fragments. Ophiuroids and ascidians use sponges and spicule mats as perches to gain access to the presumed higher water flow rates above the sediment-water interface. Six species of hexactinellids dominate the Weddell Sea shelves (Barthel & Tendal 1994). These animals structure the shelf habitats, forming 'multi-storied assemblages' (Gutt & Schickan 1998) that provide important secondary substrata for holothurians, crinoids, crustaceans and fishes.

Demospongia

Demospongia is by far the most diverse sponge group. Their skeletons are composed of 'spongin' fibres and/or siliceous spicules. They take on a variety of growth forms, from encrusting sheets living beneath stones to branching stalks upright in the water column. They tend to be large and only exhibit the more complex 'leucon' grade of organisation. Demosponges are inhabited by a wide diversity of invertebrates and have been referred to as 'veritable liv-

Table 11. Percentage of colonies containing associated species and average number of associate taxa per sponge for the different genera.

Genus	% with associated species	No. of taxa per sponge
Geodia	28.6–56.3	0.3–4.3
Phakellia	56.8–94.9	1.1–2.5
Tragosia	78.6	1.3
Isops	87.1	4.4
Stryphnus	100	7.9
Thenea	97.2–97.7	9.7–12.0

ing hotels' (Klitgaard 1995). The majority of investigations originate from shallow water in warm areas and studies on associates of deep-sea demosponges are rare (Klitgaard 1995). Klitgaard (1995) reports associated fauna of 11 species (family Geodidae) from 157–780 m water depth off the Faroe Islands. Of the 411 individuals observed in the laboratory, 324 (80%) had associates, most of them (95%) epifaunal and the remainder cryptofaunal (Table 11). Dominating groups of associated taxa were: Polychaeta (26%), Bryozoa (13%), Nematoda (11%), Ophiuroidea (7%) and Amphipoda (6.6%). The 'furry'

taxa, *Stryphnus* and *Thenea,* had the largest number of associates. Ilan *et al.* (1994) collected three species of sponges off the Israeli Mediterranean coast from a depth of 830 m: *Bubaris sarayi* sp. nov., *Sarcotragus cf. muscarum*, and *Ircinia cf. retidermata*. The sponge cavities contained the polychaetes *Harmothoe spinifera, Ceratonereis costae, Leonnates jousseaumei,* and the snapping shrimp *Synalpheus gambarelloides*. The sponge surface was encrusted with the serpulid tubeworm *Hydroides heteroceros.* For all the species, the present finding constitutes a great extension of their known depth range; this is also the first record of Lessepsian migrants from great depths.

Xenophyophores and other large testate protists

Structural attributes

Xenophyophores are giant protists that are confined to habitats deeper than 500 m and build agglutinated tests up to 10 cm or more in size (Fig. 12-1). According to recent molecular studies, at least two xenophyophore species are foraminiferans (Pawlowski *et al.* 2003; Lecroq *et al.* 2009a). They occur at bathyal, abyssal and hadal depths, but are most common where the particle flux to the sea floor is enhanced under productive
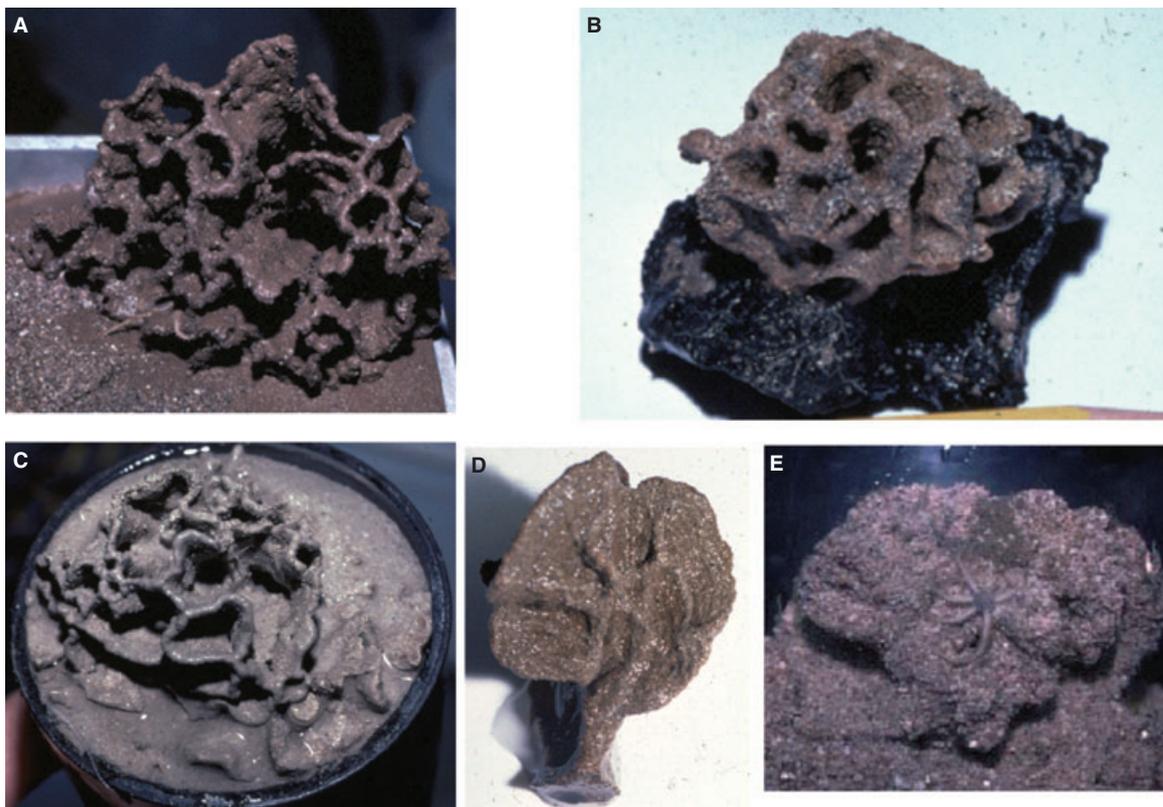
Fig. 12-1. Xenophyophores from soft and hard substrate on eastern Pacific seamounts. (E) *Galatheammina* with an asteroid aboard.
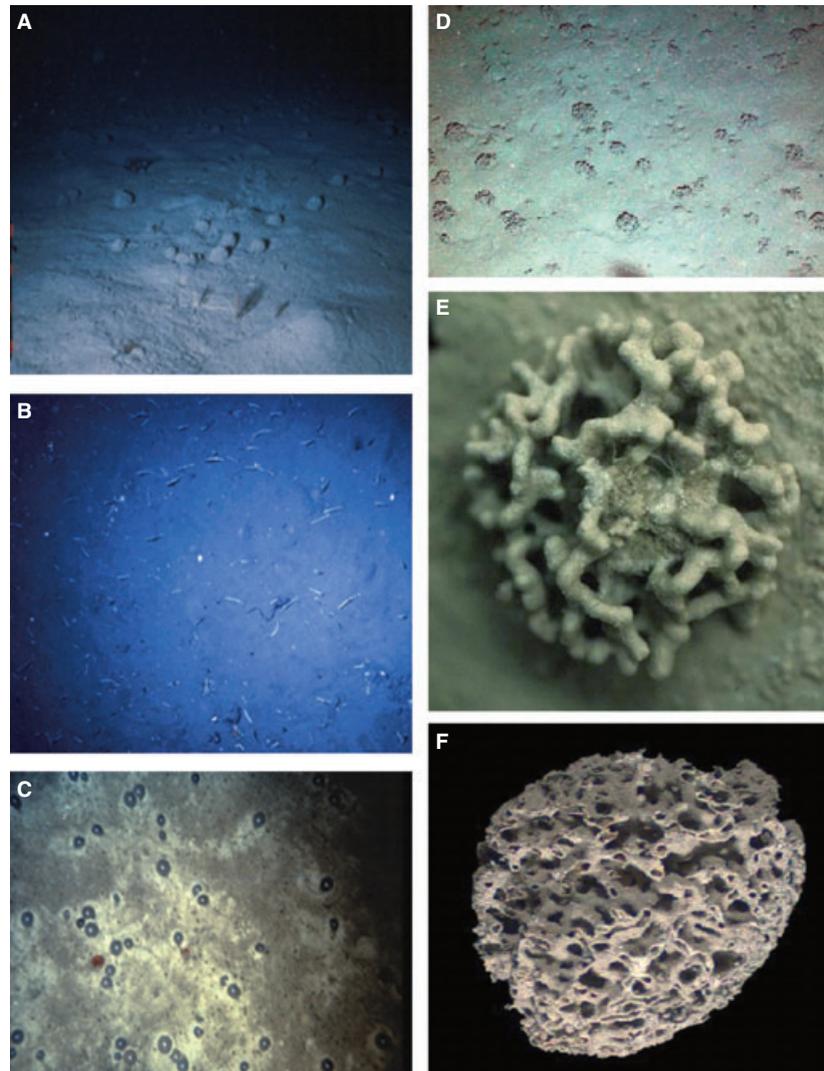
Fig. 12-2. (A) Xenophyophores (*Syringammina*) at 1250 m, NW Atlantic margin; Photograph by B. Hecker. (B) Foraminifera (*Bathysiphon filiformis*) at 850 m on the margin off North Carolina, USA (C) *Gromia sphaerica* on the Oman margin; photograph by C. Smith and D. Hoover. (D) Xenophyophores (*Reticulammina)* from Nazare Canyon (4300 m Portuguese margin). (E) Xenophyophore *Reticulamina* sp. Porcupine Abyssal Plain, NE Atlantic (4850 m) with associated isopod. (F) Xenophyophore (*Syringammina fragilissima*) from Rockall Trough (950 m NE Atlantic).

regions, in canyons, on areas of raised topography such as seamounts and ridges, or on continental slopes (Tendal 1972; Levin 1994). Some species attach to hard substrates, but many live in soft sediments primarily as epifaunal forms, although there are some infaunal species. On seamounts and some slopes, the epifaunal species can be the most visually conspicuous and abundant large organisms on the ocean floor. Fist-sized tests of *Reticulammina* and *Syringammina,* which reach densities of 1–36 individuals per m^2 on continental slopes and seamounts (Fig. 12-2), can represent an important source of habitat heterogeneity (Levin *et al.* 1986; Levin 1991; Levin & Gooday 1992; Hughes & Gooday 2004).

There are two xenophyophore orders, the Psamminida with rigid tests, and the Stannomida, characterised by proteinaceous threads that ramify the soft, flaccid test. The test morphologies range from spherical to plate-like or tubular, but more complex, branched, folded or reticulated morphotypes are also common among the psamminids. These complex forms in particular provide a variety of microhabitats for smaller organisms. Xenophyophore tests typically extend several centimeters above the surrounding level bottom, thereby providing their pseudopodia with access to enhanced water current velocities and enhancing their potential for suspension feeding and particle trapping. Documentation of ^{234}Th inventories in tests 3–17 times above background sediment on seamounts, suggests that the baffle-shape of the psamminid tests entrains fine, organic-rich particles, and possibly larvae as well (Levin & Gooday 1992).

The internal organisation of xenophyophores includes branching, multinucleate cytoplasm enclosed within an organic tube (called the granellare system) and faecal pellets (stercomata) retained within the test as distinct
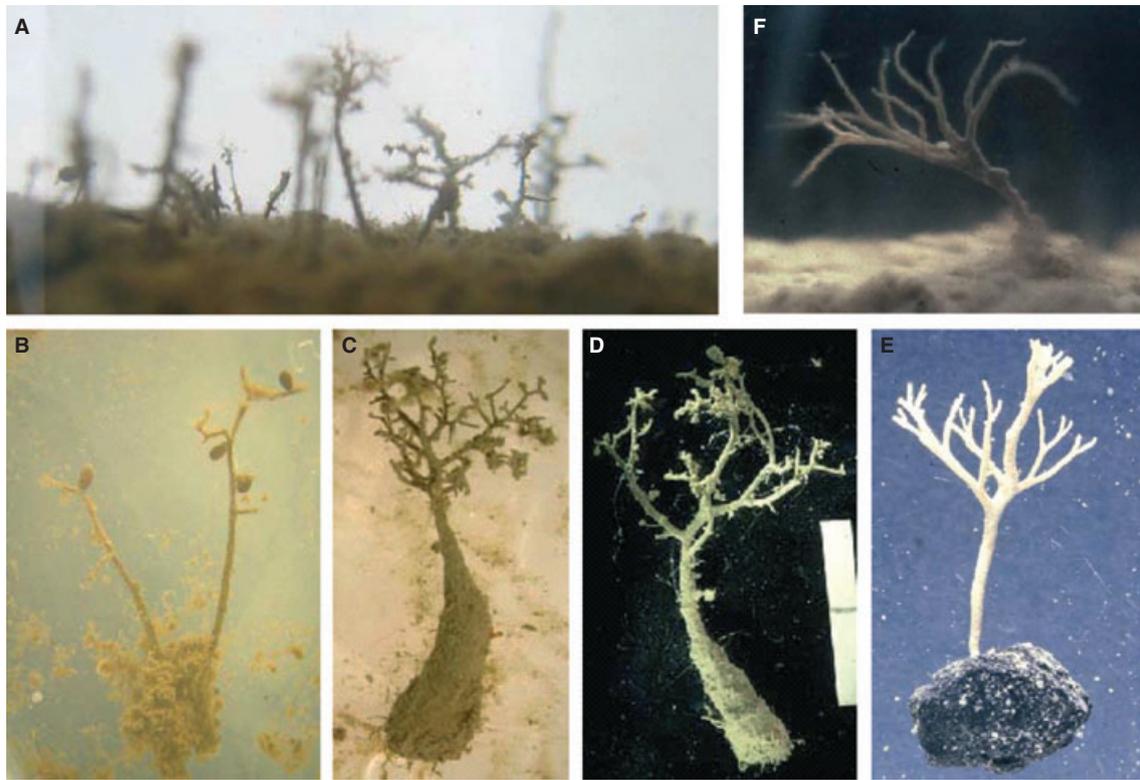
Fig. 12-3. Arborescent foraminifera. (A) *Pelosina* sp., Pakistan margin, Arabian Sea (1000 m). (B) Same site showing grape-like gromiids (*Gromia pyriformis)* attached to branches. (C) *Pelosina* sp. from Nazare Canyon, Portuguese margin (1415 m). (D) *Pelosina* sp. from North Carolina margin (850 m). E) Unidentified species attached to dropstone, BIOTRANS site (4550 m). (F) *Arborammina hilaryi* Madeira Abyssal Plain (4950 m).
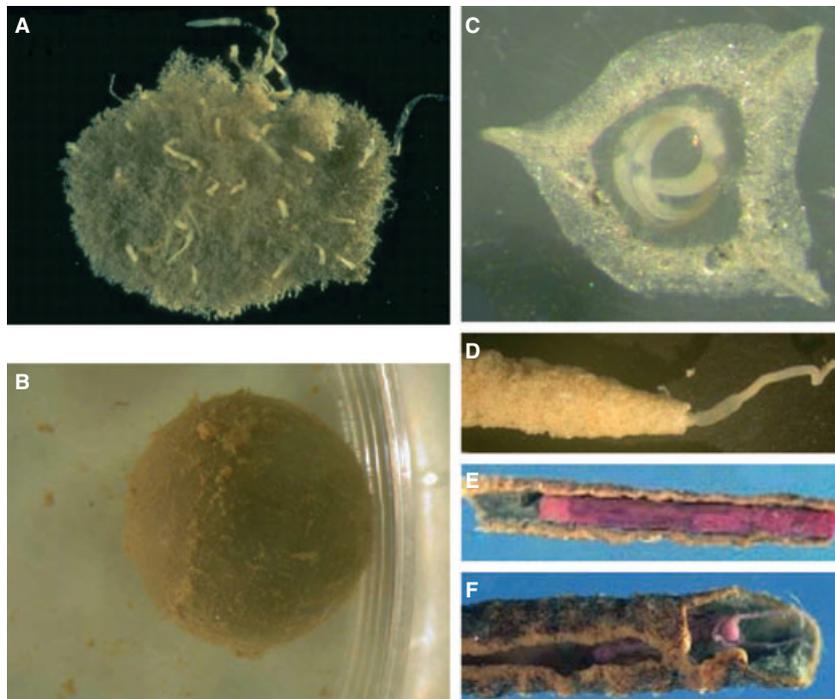
Fig. 12-4. (A) The bryozoan *Nolella* intergrown with the komokiacean *Lana* sp.(NW African margin, 4450 m), (B) Gromiid *Gromia sphaerica* with network of foraminiferan *Telammina* on surface (1850 m, Pakistan margin). (C) *Vanhoeffenella* with nematode (3500 m, Weddell Sea). (D,E) Tubular foraminiferans with sipunculan worms [NE Atlantic: (D) *Hyperammina* sp. from 1857 m, Whittard Canyon; (E) *Bathysiphon rusticus* from 4000 m off NW Africa]. (F) *Bathysiphon rusticus* with ischnomesid isopod (4000 m off NW Africa).

Table 12. Associations between protozoans and other organisms. Numbers indicate specimens of particular protozoan and metazoan taxa associated with the different species.

associated organisms	xenophyophores				foraminifera					gromiids
	Pacific species[a]	*Syringammina*[b]	*Aschemonella*[c]	others[d]	tubular (inside)[e]	tubular (outside)[f]	*Pelosina*[g]	*Vanhoeffenella*[h]	Komoki[i]	*Gromia* spp.[j]
protozoa										
foraminifera	ND	3647	ND	ND	*	*	*	–	*	*
gromiids	ND	–	ND	ND	–	–	*	–	–	*
metazoan macrofauna										
polychaetes	56	120	2	–	36	*	*	–	–	–
bryozoans	–		–	*	–	–	–	–	*	–
isopods	21	1	–	–	–	–	–	–	–	–
other peracarids	8	11	–	–	–	–	–	–	–	–
molluscs	8	8	–	–	–	*	–	–	–	–
ophiuroids	40		–	–	–	–	–	–	–	–
sipunculans	5	5	8	–	864	–	–	–	–	–
sponges	5	1	–	–	–	–	–	–	–	–
nemerteans	4	–	–	–	–	–	–	–	–	–
turbellarians	2	1	–	–	–	–	–	–	–	–
other taxa	4	4	–	–	–	–	–	–	–	–
metazoan meiofauna										
nematodes	174	2442	6	4	3	–	*	*	*	–
harpacticoids	148	207	–	–	–	–	–	–	*	–
ostracods	7	8	–	–	–	–	–	–	–	–
others	4	3	–	–	–	–	–	–	–	–

Data from following sources:
[a]Levin & Thomas (1998), Eastern Pacific.
[b]Hughes & Gooday (2004 – foraminifera); Van Gaever *et al.* (2004 – metazoans), both Atlantic).
[c]Gooday (1984), NE Atlantic.
[d]Gooday (1984), Gooday & Cook (1984 – bryozoans), Gooday & Tendal (1988 – bryozoans), all NE Atlantic.
[e]Gooday (1984 – metazoans), Gooday & Haynes (1983 – foraminifera), both NE Atlantic.
[f]Lipps (1983), Gooday *et al.* (1992 – North Carolina margin).
[g]Gooday & Bowser (2005), Gooday (unpublished observations), both Pakistan margin.
[h]Hope & Tschesunov (1999); Gooday & Sabbatini (unpublished observations – Weddell Sea).
[i]Gooday & Cook (1984), Shires *et al.* (1994), both NE Atlantic.
[j]Aranda da Silva & Gooday (2009), Gooday (unpublished observations), Pakistan margin.
*Presence only (*i.e.* no quantitative data). ND = no data.

masses ('stercomare') that are enclosed within an organic sheath to form the stercomare system (Tendal 1972). In many xenophyophores, the test interior is full of agglutinated particles, but more 'advanced' forms are hollow, apart from the stercomare and granellare. This test structure provides four distinct microhabitats that can be inhabited by foraminiferans and other taxa. Animals can live (i) within the remains of the organic tubes of the xenophyophore granellare system, (ii) within the branches of the test, but outside the granellare tubes, (iii) attached to the outer surface of the test, or (iv) in mud trapped between the test branches (Hughes & Gooday 2004).

Many other large deep-sea agglutinating foraminifera form tubes, tree-like structures, bushes or mudballs and protrude above the sediment surface (*e.g.* Gooday 1984; Gooday & Cook 1984; Levin 1991; Gooday *et al.* 1992) (Figs 12-3 and 12-4A,D–E). However, they rarely exceed a few centimeters in length and primarily provide harder substrate, elevation above the bottom, and attachment surfaces for associated taxa (Levin 1994).

Faunal associates
The tests of large, epifaunal xenophyophores, particularly those with complex, reticulated or folded morphologies, (Figs 12-1 and 12-2E) harbour many different kinds of metazoans and protozoans and appear to constitute faunal 'hotspots' within deep-sea sediments (Levin 1991, 1994). There is a positive relationship between test size and number of metazoan inhabitants in xenophyophores from Eastern Pacific seamounts, and it is on coarse substrates that their contribution to faunal heterogeneity is believed to be greatest (Levin & Thomas 1988).

Many taxa live within the interstices of xenophyophore tests (Table 12). Twenty-seven tests from Pacific

seamounts yielded 153 macrofaunal and 333 meiofaunal individuals. The isopod *Hebefustis* sp., which occurred in 'family' groupings within tests but were not present outside the tests, is a possible obligate associate. In addition, densities of tanaids, isopods, ophiuroids, nematodes, harpacticoid copepods and ostracods (but not polychaetes) were enhanced in sediment beneath and around the seamount xenophyophore (Levin & Thomas 1988). Hughes & Gooday (2004) analysed rose-Bengal stained (*i.e.* 'live') foraminifera associated with dead tests of the large xenophyophore *Syringammina fragilissima* in the Rockall Trough (NE Atlantic; 950 m water depth). This species builds a test with hollow branches that anastomose to form a complex, reticulated structure (Fig. 12-2F). Four tests yielded, in total, 3647 rose-Bengal-stained foraminiferal specimens representing 259 species, with 352–2238 specimens and 63–153 species found in each test. Many were common bathyal species that also occurred in the surrounding sediment. However, others, including the organic-walled monothalamous *Cylindrogullmia* sp. and the calcareous *Chilostomella elongata*, were more or less confined to the xenophyophores. The *Syringammina* tests also yielded between 175 and 1217 metazoans per test (total 2829) (Table 12). Nematodes, the dominant taxon, were identified to genus level (Van Gaever *et al.* 2004). Each test yielded 29–59 genera, significantly fewer than in the underlying or adjacent sediments. Among those present in the xenophyophores but rare in the adjacent sediment were *Syringolaimus*, *Viscosia* and *Paracanthonchus*. These are all large nematodes with prominent teeth, suggesting that they are predators. Other dominant taxa associated with *Syringammina* tests, such as *Trefusia*, *Halalaimus* and *Acantholaimus*, were also found in the sediments, albeit in lower relative abundances. The nematodes showed a high variability with different dominant genera (*Syringolaimus*, *Trefusia* and *Halalaimus-Acantholaimus*) present in each of the three tests. Thus, large xenophyophore tests can provide a microhabitat for particular nematode taxa that are less prominent, or even absent, in adjacent deep-sea sediments.

Other agglutinated foraminifera, particularly those with large tubular tests (*e.g. Bathysiphon, Hyperammina, Rhabdammina, Pelosina*), often harbour metazoans and other protists, while their exterior surfaces provide substrates for sessile organisms, notably other foraminifera, but also polychaetes (Table 12, Figs 12-3 and 12-4A,D–E). On some continental margins, tubes of *Bathysiphon, Hyperammina* and *Rhabdammina*, many of them dead, accumulate in large quantities at the sediment surface (Linke & Lutze 1993; Gooday *et al.* 1997). We speculate that these thanatocoenoses provide an important source of habitat structure for metazoans, particularly vermiform and sessile taxa. Smaller foraminifera can also provide habitat struc-

ture; for example, monothalamous tests of *Vanhoeffenella gaussi* are sometimes occupied by juvenile nematodes (Hope & Tchesunov 1999) (Fig. 12-4C). Even gromiids, close relatives of the foraminifera, can be colonised by other organisms, notably sessile foraminifera, despite the fact that they have smooth, organic test walls (Aranda da Silva & Gooday 2009; Fig. 12-3C). Komokiaceans can also harbour metazoans, including the ctenostome bryozoans, which intergrow with the tubules of these large foraminifera (Gooday & Cook 1984) (Fig. 12-3B).

Few experimental studies address the nature of interactions between large agglutinated protozoans and their metazoan and protozoan associates. Provision of substrate, enhanced food supply, refuge from predators, nursery habitat and breeding habitat have all been suggested as benefits to biota associated with large, agglutinated tests in the deep sea (Levin *et al.* 1986; Levin 1991). It is also possible that some foraminifera or animals present within or beneath tests were passively entrained from the overlying water as larvae or propagules.

Associations between large protists and microbiota may take many forms. Tendal (1972) proposed that xenophyophores garden bacteria within stercomes. Enhanced respiration rates (Deming unpublished in Levin & Gooday 1992), together with elevated bacterial fatty acids within xenophyophores (Laureillard *et al.* 2004), support this hypothesis. A recent molecular study suggests that komokiaceans are hotspots of microbial diversity. Lecroq *et al.* (2009b) detected DNA sequences attributable to Radiozoa, Haplosporidia, dinoflagellates, diatoms, fungi and Apusozoa associated with komokiacean foraminifera (*Septuma, Normanina*). They suggested that at least some of these organisms were inhabitants of the komokiaceans. Fungal sequences, for example, were confined to the komokiaceans and absent from the surrounding sediment.

Corals and sponges as fish habitats

The relationship between fish distribution and reef environments in the deep ocean has been confounded by the lack of data and the qualitative nature of the data resulting from indirect sampling. Deep-water coral regions have been suggested to provide shelter, enhanced food supply, spawning habitat and nursery grounds for associated fish species, and are of particular importance in deeper waters where there are fewer three-dimensional habitats (Fosså *et al.* 2002; Husebø *et al.* 2002). It has also been hypothesised that these features may enhance local productivity and concentrate exploitable resources (Ross & Quattrini 2007). An overview of fish species related to corals and sponges is provided in Appendix 2.

Several studies have shown aggregations of commercially important fish related to *Lophelia* reefs (Mortensen *et al.* 1995; Furevik *et al.* 1999; Fosså *et al.* 2002; Freiwald *et al.* 2002). In particular, the redfish (*Sebastes* sp.) is common on reefs, both at the top (Freiwald *et al.* 2002) and on coral rubble (Mortensen *et al.* 1995). Stone (2006) reported that 85% of the economically important fish species observed in coral habitat in the Aleutian Islands, Alaska, are associated with corals or other emergent epifauna. Open habitats had the lowest densities of commercially important species and juvenile redfish, and it was concluded that there was a strong facultative use of corals and emergent epifauna. Furevik *et al.* (1999) reported that long-line catches of redfish, ling and tusk can be significantly greater on reefs compared to non-reef areas. Husebø *et al.* (2002) set long-lines off Southwestern Norway (150–350 m) in coral habitats and found that significantly more fish were caught in the coral reef habitats, and these were generally larger than those caught in the non-coral areas. Hall-Spencer *et al.* (2002) reported 13 species of fish in commercial deep-water fish trawls from 200 m depth off West Norway, and 840–1300 m off the west coast of Ireland, all of which contained large fragments of coral that had been broken from reefs.

Ross & Quattrini (2007) have probably presented one of the strongest cases for the association of fish with cold-water corals. Their data from manned submersible dives and otter trawls conducted on the Southeastern United States slope (356–910 m) indicated a strong association between coral habitat and fish presence. Most species were observed on prime and transition reef habitats with the off-reef habitats, providing a well developed, different fauna. The study stresses the need for quantitative data on fish communities from reef areas using a range of techniques to derive firmer conclusions concerning fish-coral associations in the future. A comparable study by Costello *et al.* (2005) on *Lophelia* reefs across eight sites in the northeast Atlantic observed 25 subspecies, 17 of which are of commercial importance. A total of 92% of these fish species and 80% of individual fishes observed were considered to be reef-associated. Interestingly, depth was determined as the most significant parameter influencing the species present, and this has been found in many off-reef demersal fish studies in topographically complex environments (King *et al.* 2006; Bergstad *et al.* 2008).

Several studies have indicated an association between fishes and gorgonian corals. The large gorgonians *Primnoa resedaeformis* and *Paragorgia arborea* are a preferred habitat of redfish (*Sebastes* spp.) and they may offer shelter against strong near-bottom currents and predators (Mortensen *et al.* 2005). Off Alaska, at 161–365 m,

Krieger & Wing (2002) found that 85% of the larger rockfish (*Sebastes* spp.) were associated with gorgonian corals (*Primnoa* spp.). Similarly, Heifetz (2000) found that some species, namely redfish and atka mackerel [*Pleurogrammus monopterygerygius* (Pallas 1810)], were the most common species caught with gorgonian, cup and hydrocorals, and that there were different species caught with soft corals. Messing *et al.* (1990) conducted submersible dives on the western margin of the Little Bahama Bank (500–700 m) and found that most individual fish observed occurred on the steep flank of the reef and the reef crest. Large, paired wreckfish (*Polyprion americanus* (Bloch & Schneider 1801)) were hypothesised to be present on the larger lithoherms, and a potential ophidiid or bythitid was consistently associated with the gorgonian *Gerardia* species.

Not all studies have reported positive associations between fish and cold-water coral habitat. Auster (2005), using fish census ROV data from the Gulf of Maine, found that habitats dominated by dense corals and epifauna are functionally equivalent to other, less complex habitats, such as boulders with sparse coral cover. In particular, sites with dense coral and epifaunal habitats supported only moderate levels of fish diversity when compared with other sites considered. Tissot *et al.* (2006) concluded, from 112 submersible dives at 32–320 m off southern California, that structure-forming invertebrates and fishes were found in the same habitats, but that there is not necessarily a functional relationship.

Reef-building sponges also create habitat for other organisms and fish. They are known to provide refuge for adult redfish and nursery habitat for juveniles in the Georgia Basin, Canada (Cook *et al.* 2008). Abundances on live reefs *versus* dead reefs have been observed to be five times higher in the Queen Charlotte Basin, Canada (Cook 2005). Juvenile redfish have been specified by Freese & Wing (2003) as fortuitous sponge dwellers, category 4, within a series of definitions laid down by Tyler & Bohlke (1972) to categorise sponge-associated fauna. Freese & Wing (2003) used a submersible to survey sea-floor habitat and associated benthos in the Northeastern Gulf of Alaska. Two-thirds of the boulders had sponge (*Aphrocallistes* sp.) colonies. Eighty-two juvenile (5–10 cm) red rockfish (*Sebastes* sp.) were observed closely associated with the sponges. No juvenile red rockfish were seen in proximity to boulders without sponges, nor were any observed on the sand-silt substrate between boulders.

As discussed by Ross & Quattrini (2007) and Roberts *et al.* (2009), there are currently many methodological difficulties associated with sampling deep-sea, coral-associated fish density and diversity that need to be addressed and improved. Of specific importance is how data are

obtained on habitat use. The importance of cold-water corals as essential fish habitat is difficult to demonstrate. The evidence presented within the primary literature suggests that deep-water fish species do utilise coral habitats. However, the level of their association and dependence varies geographically and is ultimately influenced by the natural variability of the cold-water coral reef environment (Roberts *et al.* 2003).

Synthesis

Functional roles of biotic habitat and diversity consequences

To a large extent, the added heterogeneity provided by habitat-forming organisms is related to depth. Below 2000 m, firm substrate and food supplied by currents are limited resources. Here, habitats are provided by relatively small organisms, *e.g.* glass sponges, polychaete tubes, stalked crinoids and xenophyophores 5–25 cm in height or diameter. In many areas, these organisms offer the only available firm and elevated substratum giving access to food particles transported in the logarithmic part of the benthic boundary (Fig. 7). At shallower sites (<600 m), shelter against predators and currents, together with firm substratum and increased food supply, are the main resources provided by the larger organisms that form biotic structures such as coral and sponge reefs.

Habitat-forming organisms often incorporate several microenvironments that provide different resources for different faunal groups. Thus, sessile taxa and detritivores, including polychaetes and hydroids, as well as secondary associates (mainly crustaceans) tend to inhabit older and dead parts of the host organism, whereas mobile predators or filter feeders (shrimps and ophiuroids) inhabit the upper and younger parts of the host. As a result, the highest diversity is associated with old and dead parts of corals and glass sponges. Here, we also find secondary associates connected to the substratum provided by associated colonial organisms, *e.g.* hydroids and bryozoans.

Many organisms are associated with corals and sponges (Jensen & Frederiksen 1992; Barthel & Gutt 1992; Klitgaard 1995; Buhl-Mortensen & Mortensen 2005). In a recent review, Buhl-Mortensen & Mortensen (2004a) report 983 macro-invertebrate species from 74 deep-water coral species. However, most of the coral and sponge associates are also present in the background community or are known from other habitats (Klitgaard 1995; Jensen & Frederiksen 1992; Mortensen & Fosså 2006), suggesting that regional diversity may not be enhanced substantially by the presence of these large, habitat-forming organisms.

There are too few studies of xenophyophores and other large agglutinated foraminifera to determine the extent to which they host specialists. Most associations are probably incidental rather than obligate. Some inhabitants, for example the sipunculans and ischnomesid isopods sometimes found inside tubular foraminifera (Fig. 12-4D–F), typically inhabit sheltered microhabitats, irrespective of their nature (*e.g.* Wolff 1979, 1980). It is possible, however, that a few sipunculans, nematodes and isopods are specialist inhabitants of foraminifera (Gooday 1984; Hope & Tchesunov 1999) and xenophyophores (Levin & Thomas 1988; Van Gaever *et al.* 2004).

Obligate relationships between associated species and coral hosts are more common for octocorals than for scleractinians. The reason for this is not known. Symbiosis in cold water corals involves both parasitism and mutualism (cleaning and protection against predators) (Mortensen 2001; Buhl-Mortensen & Mortensen 2004a).

Comparison of associates among host taxa

Symbionts (both obligate and facultative) are reported from 74 species of deep-water corals: 33 gorgonians, 29 scleractinians, 7 alcyonaceans, and 5 antipatharians (Buhl-Mortensen & Mortensen 2004a). The highest number of symbiotic species (65) was found for gorgonians. Fifty-three species were found with scleractinians, whereas alcyonarians and antipatharians both had five species each. Twenty-nine percent of the symbionts on deep-water gorgonians were obligate, whereas the comparable number for scleractinians was 11%. Cirripedia was the most species-rich group in gorgonians, whereas for scleractinians, crustacean decapods were as species-rich as cirripeds. For antipatharians, polynoid polychaetes were the richest group of commensals, represented by three species. No taxonomic groups were typical for the alcyonarians.

Comparison of deep- *versus* shallow-water corals

A high level of diversity is associated with shallow-water reef communities (McCloskey 1970; Connell 1978). Few faunal studies address more than one of the different habitats found in this biotope because of the taxonomic challenges and complex habitat structure. Based on available literature on obligate invertebrate symbionts in shallow-water corals, Buhl-Mortensen & Mortensen (2004a) recorded 311 species from 210 coral species. Facultative symbionts of shallow-water corals were not included in their review, but the number is still much higher than that for deep-water corals (Table 6). Although more than 980 species have been recorded on deep-water corals, only 112 of these can be characterised as symbionts, of which

30 species are obligate to various cnidarian taxa (Buhl-Mortensen & Mortensen 2004b).

Many species, including gastropods, feed directly on the tissues of warm-water gorgonians (Goh *et al.* 1999). Suspension feeders, which use the host as a platform for filtering particles from the passing water currents, dominate the associated fauna of *Primnoa* and *Paragorgia*. The cold-water scleractinian coral *Lophelia pertusa* harbours similar associates (Jensen & Frederiksen 1992; Mortensen & Fosså 2006). In contrast, associates of warm-water and tropical corals are dominated by deposit feeders utilising the mucus and detritus deposited in old parts of the coral-heads as a food source (McCloskey 1970; Patton 1976; Reed *et al.* 1982).

Raes (2006) showed that although the environmental conditions in tropical and deep-water coral biotopes are fundamentally different, the nematode communities (genus level) associated with them are determined generally by the same factors: microhabitat types, the influence of current activity and sediment infill. Both in tropical and cold-water coral degradation zones, there is a distinction between sediment communities and communities associated with large biotic substrata (coral and sponge skeletons). These latter communities are characterised by high abundances of Epsilonematidae and Draconematidae. On the other hand, communities in both biotopes were distinctly different from each other, as they were clearly influenced by local assemblages. The same author also concluded that nematode assemblages in cold-water coral degradation zones (coral rubble) are at least as diverse as those in tropical coral degradation zones, and might even be slightly more diverse. For the associated harpacticoid copepod fauna of tropical and cold-water coral substrates, species richness and evenness in the deep sea were even higher than in the tropical habitat.

Biogenic structures, climate change and human interactions

The human imprint is steadily moving into deeper and deeper waters in ways that will affect biotic structures and their habitat provision services. Trawling, mining, energy extraction and waste disposal all now occur at slope and sometimes even at abyssal depths (Glover & Smith 2003; Smith *et al.* 2008a,b; Levin & Dayton 2009). Deep-sea fishing extends to depths of >1000 m and has recently been shown to impact fish stocks indirectly down to at least 2600 m (Bailey *et al.* 2009). The destruction by trawling of reefs made by large, habitat-forming species in the deep sea is well documented (Hall-Spencer *et al.* 2002; Roberts 2002; Baco *et al.* 2009). Coral integrity is threatened by expanding petroleum exploration and fishing activities that overlap with the distributions of black (Antipatharia), horny (Gorgonacea), stony (Scleractinia-

ria) and soft corals (Alcyonaria) (Mortensen *et al.* 2006). The impact of fishing on fragile deep-water coral reefs is distressingly clear in sea-floor photographs that show reefs reduced to fragments by the action of trawl doors being dragged across the sea floor (Roberts *et al.* 2000). On seamounts to the south of Tasmania, intact corals were found only on unfished or very lightly fished seamounts. Trawling had stripped corals from heavily fished seamounts, leaving a substrate that consisted mainly of bare rock and pulverized coral rubble (Koslow *et al.* 2001). Unfished seamounts yielded 106% greater biomass and 46% more species per sample than heavily fished seamounts, indicating that the fauna associated with the coral is also heavily impacted. Similar effects are reported for other Pacific seamounts (Clarke & Rowden 2009). More than a quarter (29–34%) of seamount species in the Southwest Pacific are possible endemics (Richer de Forges *et al.* 2000), suggesting a likely impact of fishing on regional as well as local diversity. Destruction of deep-water corals is also well documented on the Northwest European margin (*e.g.* Hall-Spencer *et al.* 2002; Wheeler *et al.* 2005 and references therein). Even though the fauna of the reefs is mainly non-endemic (Mortensen & Fosså 2006), they represent local diversity hotspots, and may serve as species pools with importance for the biodiversity in a wider area than just the reefs.

Climate change is a more subtle, insidious form of human impact. It is becoming clear that the secondary consequences of atmospheric CO_2 rise and global warming have the potential to impact large areas of deep ocean (Smith *et al.* 2008a,b). In particular, acidification resulting from CO_2 uptake by the ocean is leading to reduced aragonite and calcite saturation states. These will have the greatest effects on organisms with aragonitic skeletons, including cold-water corals, and will be particularly severe in the North Pacific, where carbonate saturation states are already low (Guinotte *et al.* 2006). Reduced rates of calcification, or the inability to persist at all, are likely responses over the coming century. At the same time, ocean warming is elevating respiration and increasing stratification, both of which exacerbate oxygen depletion. Many areas of the tropical and Northeast Pacific have declining oxygen levels, particularly in tropical areas and at depths of 200–700 m, with shoaling of the upper boundaries of oxygen-minimum zones (Stramma *et al.* 2008; Bograd *et al.* 2008). Most of the habitat-forming taxa discussed in this paper, including sponges, corals and xenophyophores, appear to require significant water flow and oxygenation, and are largely absent from oxygen-minimum zones (Levin 2003; Gooday *et al.* 2009). As these structures can provide key nursery habitat for fishes (*e.g.* Cook *et al.* 2008), their loss could have widespread and severe consequences for fisheries health (McClatchie S.,

Goericke R., Cosgrove R., Vetter R., unpublished data). Because warmer temperatures, declining saturation states, lower pH and lower oxygenation will all occur together in many parts of the deep ocean, there is a need to evaluate how multiple stressors affect habitat-forming biota and their interactions with associated species. Increased susceptibility to parasitism or bioerosion and subsequent loss of diversity-sustaining functions interacting with physical damage from fishing could lead to the homogenization of slope habitats and the formation of barrens if conservation measures are not put in place.

Future questions and directions

Awareness of the ecological importance of deep-sea corals is growing rapidly. We have learned that colonial corals provide important habitat and could play a critical role in the life history of many marine species, including some of commercial interest (Rogers 1999; Buhl-Mortensen & Mortensen 2005; Mortensen *et al.* 2005). This has led the conservation community to call for the establishment of marine protected areas (MPAs) to protect important coral habitats and services (Hall-Spencer *et al.* 2002; Mortensen *et al.* 2005). To effectively conserve biotic habitat-forming resources, future research must address the following issues.

1   Basic information is required about the nature and distribution of habitat heterogeneity generated by biogenic structures. This applies particularly to habitats that are difficult to access, such as the vertical, sometimes overhanging sides of submarine canyons where rocky substrates are often covered in profuse growths of corals and other large sessile organisms. These can only be examined using ROVs or manned submersibles.

2   The prevalence of obligate associates must be investigated, particularly of taxa such as the xenophyophores, for which relatively little information is available.

3   The effects of ocean acidification on deep-sea organisms with carbonate skeletons, notably the cold-water corals that are particularly sensitive to declining pH levels, require urgent evaluation (Turley *et al.* 2007). The impact of acidification on reef formation and persistence is the subject of considerable uncertainty (Guinotte *et al.* 2006).

4   Many species associated with biogenic structures are of macrofaunal size. The smaller-sized organisms, the meiofaunal and particularly the microbial communities, are not well studied. In the case of microbes (prokaryotic and eukaryotic), molecular approaches offer the most obvious way forward.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix SI. List of symbiotic invertebrates and their host deep-water corals (Alcyonacea, Antipatharia, Gorgonacea and Scleractinia).

Appendix S2. Fish species that have been observed in coral and sponge habitats and are discussed in this paper.

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