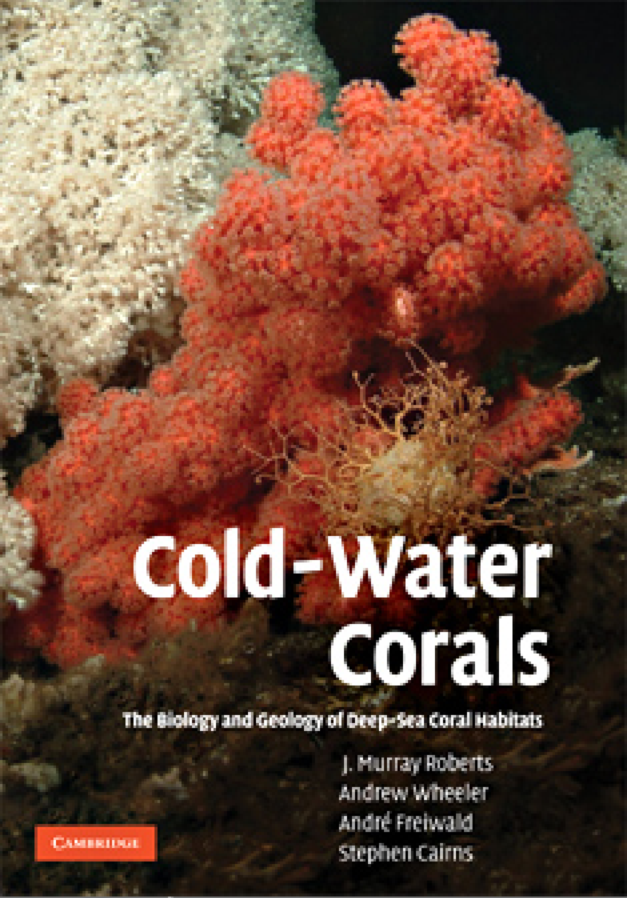

Cold-Water Corals

The Biology and Geology of Deep-Sea Coral Habitats

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Andrew Wheeler
André Freiwald
Stephen Cairns

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COLD-WATER CORALS: THE BIOLOGY AND GEOLOGY OF DEEP-SEA CORAL HABITATS

There are more coral species in deep, cold waters than in tropical coral reefs. This broad-ranging treatment is the first to synthesise current understanding of all types of cold-water coral, covering their ecology, biology, palaeontology and geology. Beginning with a history of research in the field, the authors describe the approaches needed to study corals in the deep sea. They consider coral habitats created by stony scleractinian as well as octocoral species. The importance of corals as long-lived geological structures and palaeoclimate archives is discussed, in addition to ways in which they can be conserved. Topic boxes explain unfamiliar concepts, and case studies summarise significant studies, coral habitats or particular conservation measures. Written for professionals and students of marine science, this text is enhanced by an extensive glossary, online resources (www.lophelia.org/coldwatercoralsbook), and a unique collection of colour photographs and illustrations of corals and the habitats they form.

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To our families:

Lea-Anne, Hannah and David Roberts;

Moira, Nessa, Malachy and Penny Wheeler;

Alexander, Christina, Jannik, Jule, Lea and Angela Freiwald;

Peggy, Peter and Jennifer Cairns.

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Online appendix www.lophelia.org/coldwatercoralsbook.

Topic boxes and Case studies

Topic boxes

Case studies

Preface

Corals are not restricted to shallow-water tropical seas. Of the approximately 5100 coral species alive today over half are found in deep waters. Cold-water corals can be found over a tremendous range of latitudes from tropical to polar regions and from the shallows to the deep sea. We have known about cold-water corals since the mid-eighteenth century, and pioneering oceanographic expeditions in the late nineteenth century frequently recovered cold-water corals in their dredge nets. But only since the 1970s, and particularly in the last ten years, as acoustic survey techniques have improved and been applied to wider areas of the continental shelf, slope, offshore banks and seamounts have we begun to reveal the true extent of cold-water habitats around the world. In this book we try to summarise what we know about cold-water corals and capture the excitement of a field that is now growing exponentially. For instance, a literature search for the terms 'cold-water coral' and 'deep-sea coral' over the 20 years up to 1996 returned less than 300 publications whereas the same search terms for the following 10 years revealed nearly 700 (see Fig. 1).

The scientific community's fascination with cold-water corals has developed for several reasons. As sessile, suspension feeders that produce complex, sometimes long-lasting, three-dimensional structural habitat they fall at a natural confluence of biology, hydrography and geology. A few species of scleractinian cold-water corals develop elaborate reef frameworks that have spawned many studies into the processes underlying cold-water coral reef and coral carbonate mound formation. Individual cold-water corals, notably species of gold (*Gerardia*) and black (antipatharian) corals may live for over a thousand years, making them by some margin the longest-lived animals in the oceans. The skeletal remains of these corals and long-lasting reef and mound deposits now provide unique palaeoceanographic archives of intermediate water mass temperature and age.

This book's focus is on those cold-water corals that form structural habitat. We will consider how these species function as animals by reviewing what we know

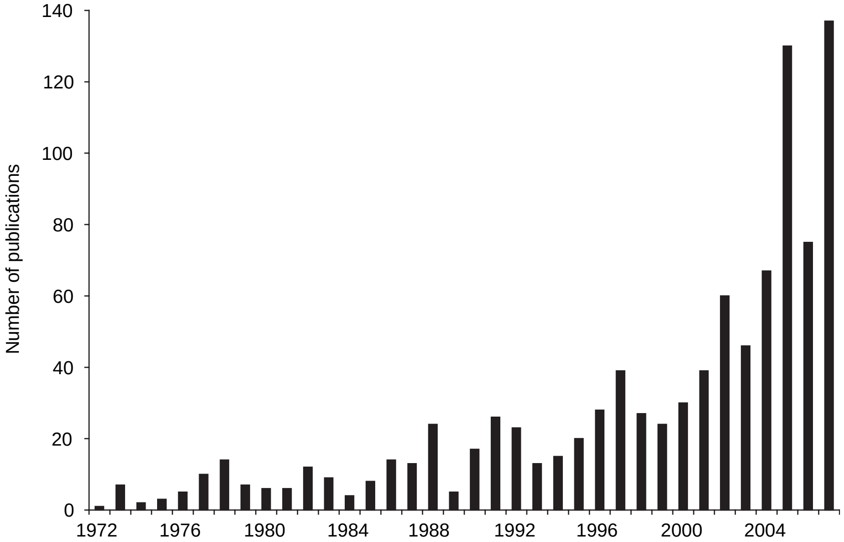

Fig. 1. Histogram showing the number of research papers referring to 'cold-water coral' or 'deep-sea coral' between 1972 and 2007. Special publications devoted to cold-water corals appeared in 2002, 2005 and 2007 explaining the higher number of papers in those years.

of their feeding, growth, reproduction and physiology. In many instances our biological understanding is limited by the practical difficulties of studying any group of animals that live at great depths far from shore. In contrast, our ability to map areas inhabited by cold-water corals is now well advanced and has revealed surprisingly extensive provinces of cold-water coral reefs and huge seabed mounds formed by multiple generations of reef development stacked one upon the other. Long, drilled cores through these coral carbonate mounds are now providing intriguing insights into their geological history and development reaching back over two million years. But corals trace their origins even further back in time and as a group have a chequered history of extinctions and radiations, often in concert with global changes in ocean carbonate chemistry (a critical issue to understand as we enter an era of ocean 'acidification' brought about as anthropogenic carbon dioxide dissolves in the oceans). We consider these long temporal aspects from the fossil record and summarise what we know of cold-water coral palaeontology and the factors underlying preservation of the corals and other animals in the geological record.

Present-day cold-water coral habitats excite interest from all who see them because, like coral habitats in warmer, shallower waters, they are structurally complex and rich with other animal species. Careful surveys with modern submersibles and remotely operated vehicles have brought back stunning images of cold-water coral habitats that have captured the imagination not just of research scientists but also members of the public and policy makers. Although work is at an early stage, we are beginning to unravel patterns underlying cold-water coral biodiversity. Some coral habitats seem important to fish populations while others may be less significant. We urgently need properly integrated biodiversity studies related back to sound taxonomy to unlock the patterns controlling species diversity in cold-water coral habitats.

However, the same surveys that brought cold-water corals to public attention have all too frequently revealed that they have been damaged by fishing activity, primarily by bottom trawling. Concern over this damage has led to the creation of several marine protected areas to conserve these habitats. At the time of writing, international discussions on high seas conservation had begun and we consider these issues and how conservation policies can be developed and enforced to protect cold-water corals from future damage. But anthropogenic activities in the deep sea are no longer limited to bottom trawling. Deep-seabed mining, for years the stuff of science fiction, is now becoming a reality and with improved subsea technologies and international demand for metals at an all-time high it seems likely to expand by exploiting mineral deposits within seabed hydrothermal vent systems. Overlying all these activities the effects of climate change may dramatically alter the marine environment. As sea temperatures warm and anthropogenic carbon dioxide is absorbed by the oceans we are witnessing a gradual shift to more acidic ocean pH. Corals, along with all calcareous organisms, face an uncertain future. Corals calcifying in deep, cold waters may be among the first to feel the effects of predicted changes in the carbonate saturation state of the seas. Ocean acidification may shift calcareous marine systems from states of growth to dissolution. Warming seawater temperatures may perturb their physiology and food supplies. It seems that we risk dramatically increasing the stresses on cold-water coral habitats just as we begin to understand and appreciate them.

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1

History and research approaches

To most people corals are synonymous with the bright, well-lit waters of tropical coral reefs. Yet in fact the majority of corals inhabit deep, cold waters across a diverse range of marine environments from inland fjords to the continental shelf, slope, offshore banks, seamounts and even the abyssal plain. While we have known about these cold-water corals for hundreds, or even thousands, of years it is only in the last ten years that research into the biology of the corals themselves, the ecology of the habitats they provide and the geology of the structures they form has gathered pace. Cold-water coral habitats are biodiversity rich. Recent work has revealed them as unique palaeoceanographic archives. Sadly all too many surveys have shown they have been damaged by human activity. In this book we have tried to summarise the many, varied and exciting developments in our understanding of cold-water corals. Research effort on cold-water corals is now increasing exponentially around the world and it has been challenging to compress this body of work into the pages of one book. Before we consider cold-water corals and some of these recent findings in more detail we begin with a brief historical summary and an outline of the research approaches used to study cold-water corals.

1.1 History

1.1.1 Early history and taxonomy

The history of modern research on cold-water corals goes back to the late eighteenth century. Among the first written records discussing cold-water corals are notes by the Right Reverend Erich Pontoppidan, Bishop of Bergen, in his 1755 book *The Natural History of Norway*. In Chapter 6, Sea-vegetables of Norway, Pontoppidan discusses one particularly fine coral specimen that was ‘entirely white, the flowers much larger than the former [specimen], some of them even exceeding a shilling; and likewise expanded like a flower in full bloom, for which singular beauty I caused a draught of it to be taken'. The accompanying drawing illustrates the species described three years later by Carl von Linné (Linnaeus) as *Madrepora pertusa* (= *Lophelia pertusa*) in *Systema Naturae*, the book that laid the foundation of modern taxonomy. Pontoppidan goes on to describe how 'The fishermen often sell coral bushes to the apothecaries at Bergen' but, although he believed it might have medical effects when taken internally, he sounded a little sceptical of its wider medicinal properties: 'that the little beads, made of coral . . . are endued with any such singular virtue that applied externally, or hung about the neck, . . . preservative against the apoplexy, the plague, and other contagions, I cannot admit, having no evidence of it, but must leave it to rest upon its own credit'. With an eye on the precious coral fishery in the Mediterranean, Pontoppidan concludes by wondering 'Possibly could white coral be brought into fashion, a diligent search might procure as great a quantity in our seas'. On the last point he was certainly correct, we now know that Norwegian waters support spectacular white coral (*L. pertusa*) deep-water reefs.

Studies of these Norwegian coral reefs began to appear just over a decade later when another theologian, Johan Ernst Gunnerus, Bishop of Trondheim (Colour plate 1) published his 1768 work *Om Nogle Norske Coraller* (*On Some Norwegian Corals*). One of his illustrations is reproduced in Fig. 1.1. Gunnerus was a pioneer of the natural sciences. He founded the Royal Norwegian Society of Sciences and Letters, was in frequent correspondence with Linnaeus and is famous for his descriptions of many animals from the basking shark *Squalus maximus* (= *Cetorhinus maximus*) to the roundnose grenadier *Coryphaenoides rupestris* and the gorgonian octocoral *Gorgonia resedaeformis* (= *Primnoa resedaeformis*).

The early days of cold-water coral research were dominated by efforts in Europe and North America to describe the variety of species dredged from the deep sea. The British naturalist Philip Henry Gosse was among the first to focus on the biology of living corals and sea anemones. His mid-nineteenth century descriptions encouraged fashionable Victorians to dabble in seawater aquaria and he summarised his work in his 1860 book *A History of the British Sea-Anemones and Corals* (Colour plate 2). Cairns (2001a) outlined the history of taxonomic research on the azooxanthellate scleractinians. The rate of coral description relates clearly to the research effort and comes in four major pulses: (1) the worldwide revision of the Scleractinia by Henri Milne Edwards and Jules Haime (1848–50); (2) the new species described chiefly by Louis François de Pourtalès, P. Martin Duncan and Henry N. Moseley from pioneering late nineteenth century deep-sea dredging expeditions (1867–81); (3) the new species described chiefly by Alfred W. Alcock, Emil von Marenzeller and Thomas W. Vaughan from

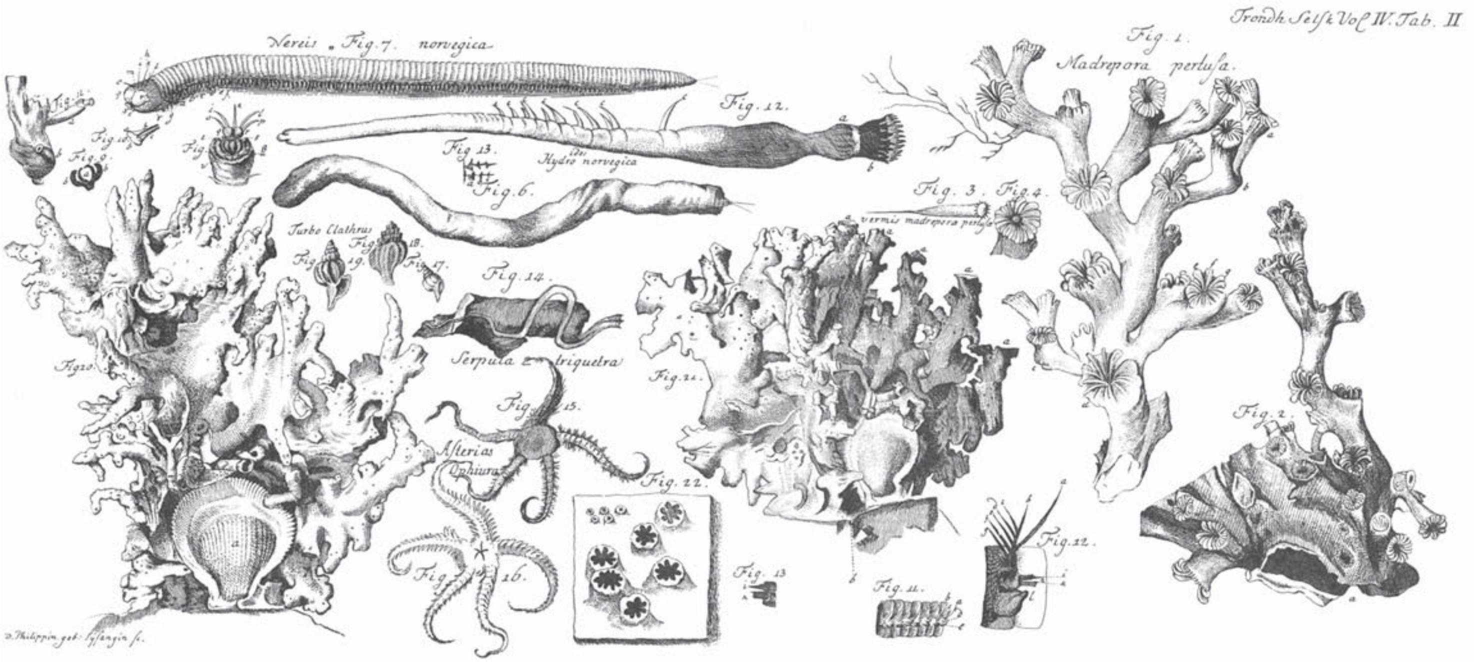

Fig. 1.1 Plate II from Gunnerus (1768) illustrates fragments of cold-water corals including *Madrepora pertusa* (= *Lophelia pertusa*) along with common associated fauna including the polychaete worm *Nereis norvegica* (= *Eunice norvegica*), gastropod molluscs and ophiuroid echinoderms.

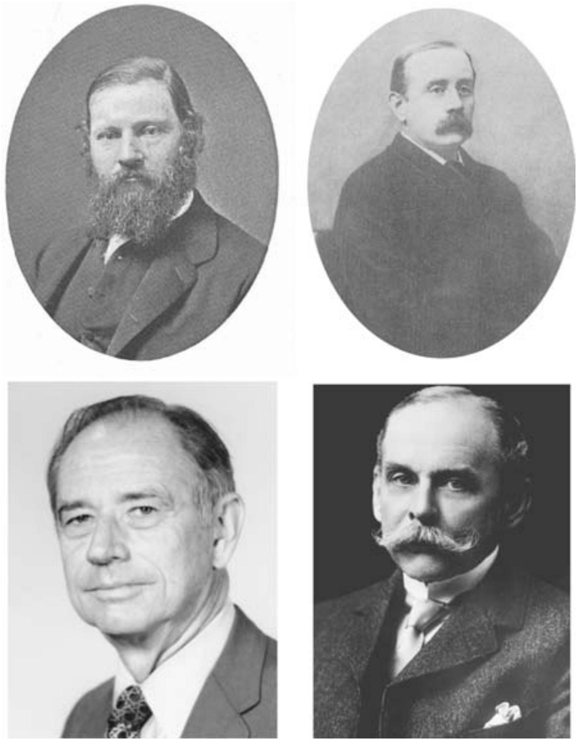

Fig. 1.2 Notable coral taxonomists, clockwise from top left: Louis François de Pourtalès (1824–80), Henry N. Moseley (1844–91), Alfred W. Alcock (1859–1933) and Frederick M. Bayer (1921–2007).

regional deep-sea dredging expeditions in the Indo-Pacific (1898–1907); and (4) the most recent pulse of descriptions based upon larger collections by vessels from France, New Zealand, the Netherlands and the USA alongside full-time research efforts by taxonomists such as Stephen Cairns and Helmut Zibrowius between 1977 and 2004. Figure 1.2 shows some notable coral taxononists.

Bayer (2001) reviewed octocoral research beginning with the first published drawings of octocoral sclerites from *Corallium rubrum* by John Ellis (1755) through to the first global monograph on ‘zoophytes’ by Peter Pallas (1766) and the critical recognition by Valenciennes (1855) that sclerites differed between species and so could be used as a taxonomic characteristic. Many of the sclerites described by Valenciennes were subsequently illustrated by Kölliker (1865). The early oceanographic expeditions of the late nineteenth century, such as that of *HMS Challenger*, greatly boosted the number of known octocoral species (Wright & Studer, 1889) and the early twentieth century saw a period of taxonomic revision by Kükenthal in his unfinished series *Versuch einer Revision der Alcyonaceen* (*An Attempted Revision of the Alcyonaceans*). In terms of deep-sea pennatulacean records, Kükenthal and Broch's (1911) description of specimens taken during the 1898–9 German *Valdivia* expedition from the eastern Atlantic to Antarctica, including the western Pacific is particularly notable, as was Kükenthal's (1919) account of the *Valdivia* Gorgonacea, which laid the foundation for his later revision of all Octocorallia in 1924. In the early twentieth century, Kükenthal recognised 141 certain and 134 doubtful species of Pennatulacea (Kükenthal, 1915) and 805 certain and 255 doubtful species of Gorgonacea (Kükenthal, 1924). Regional monographs and further species descriptions in the latter half of the twentieth century continued to add to this total. Of the approximately 3200 octocorals recognised today, around 75% are from deep waters (>50 m, see Section 2.2.4, p. 37).

Both octocoral and scleractinian taxonomy has been pursued by only a handful of scientists, often in their spare time. For example, alongside their taxonomic exploits many of the azooxanthellate scleractinian workers were primarily palaeontologists while others had a bewildering variety of jobs including school inspector, catholic priest and medical entomologist (Cairns, 2001a). Sadly this trend has if anything worsened and globally there are only a handful of coral taxonomists capable of identifying and describing cold-water corals. Many still pursue coral taxonomy in their spare time.

1.1.2 Pioneering deep-sea expeditions

The science of oceanography became established following the global expedition of *HMS Challenger* (1872–6) led by Charles Wyville Thomson and the epic collection of 50 scientific report volumes it subsequently generated under the auspices of John Murray. The impetus for the expedition had been to investigate Edward Forbes's azoic theory (based on dredging results from the Aegean Sea) that no animal life could persist below 300 fathoms (600 m). Having been to Norway and seen dredge hauls by Michael Sars rich in animal life from these and greater depths, Charles Wyville Thomson lost little time in joining forces with William B. Carpenter to set about persuading the British government to fund deep-sea dredging expeditions. These began in 1868 with the cruise of *HMS Lightning* to the waters between Scotland and the Faroe Islands. Both the *Lightning* and subsequent *HMS Porcupine* expeditions recovered cold-water corals in their dredges. These coral species were discussed in a series of papers to the Zoological Society of London and the Royal Society in the 1870s by P. Martin Duncan (Duncan, 1870, 1873, 1878).

Although less well known, the northwest Atlantic dredging expeditions co-ordinated through the Museum of Comparative Zoology at Harvard (USA) actually preceded the cruise of *HMS Lightning* by a year. Between 1867 and 1880 these expeditions covered over 600 deep-water stations recovering many cold-water coral specimens. Whereas the vessels *Lightning*, *Porcupine* and *Challenger* were converted British Royal Navy ships, the US expeditions used a series of US Coast Guard Steamers, the *Corwin*, *Bibb*, *Hassler* and *Blake*. Louis François de Pourtalès laid the foundations of North American cold-water coral taxonomy in his descriptions of the corals recovered during these expeditions (Fig. 1.3). Indeed of his 59 scleractinian coral descriptions, 47 remain valid today (Cairns, 2001a).

But it was the *HMS Challenger* expedition that revolutionised our understanding of the oceans. The dredge hauls taken during the expedition's circumnavigation of the globe put Forbes's azoic theory to rest once and for all – animal life was recovered from depths of 5500 m, an astonishing achievement at the time, and over 4000 new marine species were described. The *HMS Challenger* was built in 1858 as a Royal Navy corvette, a small, lightly armed and manoeuvrable warship. The *Challenger* sailed between survey stations and used her 1200 horse-power steam engine for dredging. Of her seventeen guns, all but two were removed to make space for laboratories and scientific sampling apparatus. Under Captain George Nares were a total ship's party of about 240 including 20 officers. There were just six scientists led by Charles Wyville Thomson (see Linklater, 1972 for a detailed history of the *Challenger* expedition). Henry Moseley, who joined as the expedition's naturalist, described the cold-water corals collected by *Challenger*. He subsequently outlined the voyage and his natural history observations in his 1879 book *Notes by a Naturalist on* HMS Challenger. Of the 48 scleractinian corals he described, 39 remain valid (Cairns, 2001a) and his skilful illustrations are among the finest available to this day (see Fig. 3.4, p. 72).

As mentioned, the dredging work of Michael Sars in Norway was part of the impetus for the *Challenger* expedition. Sars (1865) used dredging to describe coral banks formed by *Oculina prolifera* (= *Lophelia pertusa*) in Oslofjord. After the pioneering nineteenth-century expeditions established the science of deep-sea dredging on the high seas others were quick to take up the techniques of dredging and trawling and apply them through the remaining years of the nineteenth and first half of the twentieth centuries. There are many historical examples, summarised in Teichert (1958), including Dons (1944) from Norway and Joubin (1922) from the Irish and French margins.

1.1.3 The modern era begins

The next quantum leap in our understanding of cold-water corals came with the development of survey sonars after the Second World War, see Section 1.2.1, p. 13, and the use of manned research submersibles from the late 1960s and through the 1970s. After two hundred years of relying on sample material

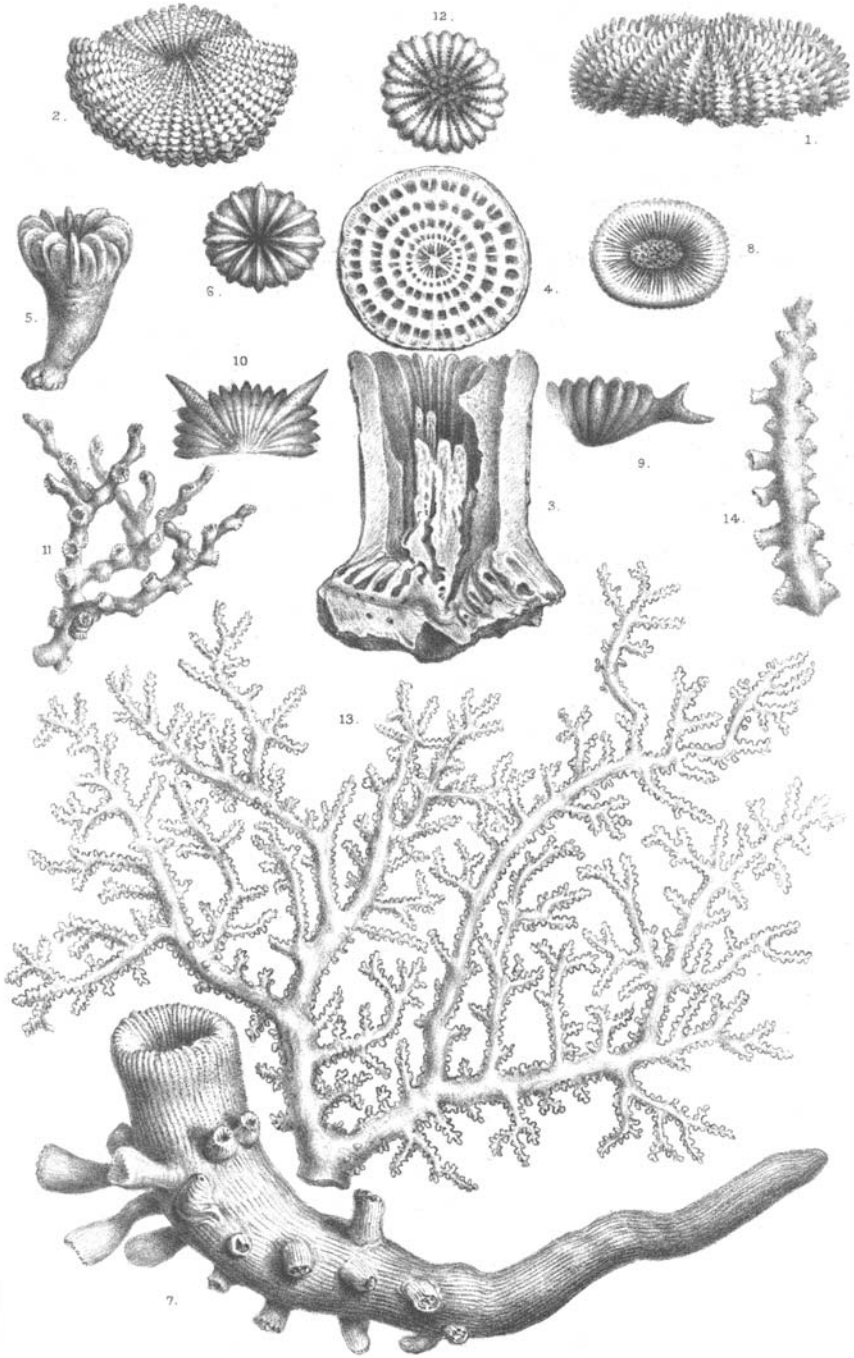

Fig. 1.3 Plate V from Pourtalès (1871) *Deep-sea Corals*, published as an Illustrated Catalogue of the Museum of Comparative Zoology at Harvard College. (1) *Diaseris crispa* (= *Fungiacyathus crispus*); (2) the same viewed

dragged from the depths and dumped onto the deck of a ship, research submersibles gave scientists the first chance to see deep-water animals in their habitats on the seafloor. The 'deep submergence vehicle' *Alvin*, named for Allyn Vine of the Woods Hole Oceanographic Institution, was brought into service in 1964. *Alvin*'s first use in cold-water coral research was to investigate mounds found on the Blake Plateau, off South Carolina (USA), following up earlier echosounder observations by Stetson *et al*. (1962). In July 1967, Milliman *et al*. (1967) dived an area of seabed mounds and found cold-water corals including *Lophelia* and *Dendrophyllia profunda* (= *Enallopsammia profunda*) along with a characteristic community of other suspension feeders. In 1971, A. Conrad Neumann dived in *Alvin* at the base of the Little Bahama Bank and northeastern Straits of Florida to depths of up to 700 m. During these dives he noted extensive areas of rocky mounds, hundreds of metres long and up to 50 m in height. These lithified mounds were richly colonised by cold-water corals and other suspension-feeding animals – subsequently Neumann *et al*. (1977) coined the term 'lithoherm' to describe them.

On the other side of the Atlantic the manned submersible *Pisces III* was used to examine cold-water corals in the northeast Atlantic (Colour plate 3). In June 1973, John Wilson surveyed *Lophelia pertusa* colonies growing on Rockall Bank and noted that they tended to form distinctive patches on the seabed, helping to explain characteristic patterns he had seen on side-scan sonagraphs. He reasoned that the colonies grew from their initial larval settlement point and gradually spread out covering a wider area, a process probably accelerated by sponge bioerosion. Using *Pisces III*, Wilson was able to document coral patches in various stages of development up to 50 m across. He subsequently summarised his observations in his classic description of cold-water coral patch development (Wilson, 1979).

The *Pisces III* submersible became infamous just two months after John Wilson's 1973 Rockall Bank dives. In August of that year the submersible was being used to help lay trans-Atlantic telephone cables approximately 100 miles west of Ireland. While being lifted back on board its mother ship, the *DE Vickers Voyager*, the submersible and its two-man crew were dropped and sank to a depth of 500 m. With life support systems for just three days an international rescue

Caption for Fig. 1.3 (cont.)
from above; (3) *Thecocyathus lævigatus* in vertical section (= *Tethocyathus laevigatus*); (4) the same in horizontal section; (5) *Desmophyllum solidum* (= *Thalamophyllia riisei*); (6) the same from above; (7) *Dendrophyllia cornucopia* (= *Eguchipsammia cornucopia*); (8) the same from above; (9) magnified portion of *Deltocyathus agassizii* (= *D. calcar*) from the side; (10) the same from below; (11) *Oculina tenella*; (12) the same from above; (13) *Stylaster filogranus*; (14) magnified branch from the same.

effort was quickly launched. Three other submersibles were flown to Ireland, *Pisces II* from England, *Pisces V* from Canada and an early remotely operated vehicle *CURV III* from the USA. After over three harrowing days several lines were attached to the stricken submersible and it was brought back to the surface. Both pilot and observer survived.

These pioneers of human exploration of the deep ocean set the stage for the work we describe in this book. Studies of cold-water corals, particularly the increased activity from the 1990s onwards, have relied on technological innovations in surveying and sampling. Many of these have been made since the 1970s, often driven by the requirements of offshore hydrocarbon development. Next we review briefly some of the methods available to cold-water coral researchers, focusing primarily on the two themes of this book, the geological and biological sciences.

1.2 Research approaches

Advances in our understanding of cold-water corals in recent decades have, in no small measure, been due to advances in submarine surveying, sampling and monitoring technologies. What was once a hostile, remote and mysterious realm is now becoming an increasingly practical area in which to observe and experiment thanks to improved deep-sea technology. Advances in genetics are also providing new insights into cold-water coral dispersal and reproduction alongside glimpses of this habitat’s microbial diversity. Likewise, advances in analytical geochemistry have allowed us to use cold-water corals as environmental archives, and helped us understand biogeochemical and diagenetic processes. Many of these advances are explored in later chapters. Here we focus on how technology has enabled us to map, sample and monitor cold-water coral habitats with a concluding comment on how future advances may allow new insights and perspectives.

As recently as the 1990s, and sometimes to this day, attempts to locate cold-water coral reefs and mounds involved sampling the seabed using low-resolution echosounder data and scattered notes of coral occurrence, often from fishing records. Even knowing exactly where the research vessel was, let alone where the sampler on the seabed was relative to the vessel, was a challenge before satellite navigation through global positioning systems (GPS). Now we can not only fix the position of the ship to within a few metres but can also locate the sample with similar accuracy using through-water acoustic ultra-short baseline (USBL) navigation transponders. Improved design means research vessels can now hold position precisely over a site using dynamic positioning (employing directional thrusters). Before this vessels were often at the mercy of wind and water currents making accurate sampling a function of informed guesswork, timing and piloting skill. With a target several hundred metres beneath the ship there was a limit to what research objectives could be achieved. Once on deck, retrieved samples were usually out of context. Scientists could identify the species and sediments present but were largely left to guess at how the animals functioned and interacted with one another. Since dredges and trawls are dragged across the seafloor they give a greater chance of hitting a patchy target but such samples contain species and sediments from a number of habitats and/or facies mixed together, and are often damaged and biased towards certain organisms or grain sizes.

Advanced technologies now enable us to produce very accurate and detailed digital maps at a range of scales, and precisely sample and observe features either in person or remotely. However, before we outline these it is worth stressing that cold-water coral habitats still challenge us; for example, the fast-flowing currents that characterise these areas impose limitations on equipment and survey design. Deep waters require strong pressure housings for instrumentation, great lengths of cable on powerful winches and large deep-sea vessels capable of getting to and remaining at remote sites for weeks on end. This all makes research cruises to cold-water coral habitats costly undertakings. Observation periods may be limited to slack waters between tides, and local currents may dictate the direction in which instruments can be towed and can make manoeuvring submersibles or remotely operated vehicles (ROVs) difficult during peak tidal flows. This imposes limitations on the work that can be carried out and can cause valuable time spent offshore to be lost.

Corals grow on hard substrata and their accumulated remains may prove difficult to sample. Coral carbonate mounds can be precipitous and lithified, limiting sampling and sometimes damaging equipment (Fig. 1.4). Cold-water coral reefs

Fig. 1.4 A ‘banana core’ bent during sampling coral carbonate mound sediment.

are both structurally and ecologically complex. Attempts to describe their structure and ecology remain challenging but technological developments allowing precise sampling with ROVs and long-term monitoring with landers and seafloor observatories are beginning to throw light on these issues. It is also important to note that while these ecosystems function seasonally, winter sea-states at high latitudes may curtail operations – often sampling, and to a lesser extent monitoring, are restricted to the fair-weather summer months.

With new technologies, the present-day cold-water coral research strategy has evolved from that of the past. The exploration phase still benefits from historical records and chance finds but now relies more on accurate regional baseline maps. These are increasingly based upon multibeam echosounder coverage with high-resolution seismic profiles (e.g. Roberts *et al.*, 2005a; see Topic box 1.1), sometimes as part of national seabed mapping initiatives. Cold-water coral reefs and mounds may become the focus of higher resolution mapping to create more accurate baseline maps using sonars deployed from ROVs or autonomous

Topic box 1.1 **Mapping with sound**

Mapping the seabed is technically more challenging than mapping terrestrial landscapes because light is readily absorbed by water, quickly negating the use of satellite remote sensing in all but the shallowest waters. Sound, on the other hand, travels great distances through water (in fact more effectively than through air) so it is possible to survey the seabed, and its underlying structure, by listening to sound reflections (or echoes) in much the same way as eyes, cameras and satellite detectors pick up reflections of light.

Low frequency (10–50 Hz) sound pulses emitted from a ship (known as industrial reflection seismics) penetrate deep into the seabed and reflect back off surfaces where there is a change in density, for example the tops of rock units or the surfaces of buried cold-water coral carbonate mounds (Fig. 1.5). The reflected echoes are received through hydrophones towed behind the ship. The depth beneath the seabed where the echo was reflected can be calculated by the difference in time between the sound pulse and its echo being received (the two-way travel time) assuming a realistic speed of sound through the seabed.

Higher sound frequencies have shorter wavelengths and can map at higher resolution allowing smaller features to be seen. But higher frequency sound does not penetrate so far into the seabed. High-resolution seismics (100 Hz–7 kHz) are ideal for mapping shallow buried (typically less than 200 m) cold-water coral carbonate mounds (Fig. 4.18). At even higher frequencies (greater than 30 kHz) most of the sound reflects directly off the seabed. By recording seabed echoes coming from either side of, as well as directly below the ship, a swath (or strip) of seabed can be imaged. Distance port and starboard from the sonar can again be calculated by time delay: the

Topic box 1.1 (cont.)

further port or starboard, the later the echo will be received. This is the principle of side-scan sonars, which are usually towed behind the vessel where it is acoustically quieter and also closer to the seabed (if desired). Higher frequencies (usually up to 500 kHz) create higher resolution images but with narrower swath, so give less coverage. The strength of the echo depends on the nature of the seabed: weak echoes return from smooth, soft seabeds and strong echoes return from rough, hard seabeds like cold-water coral reefs.

Multibeam echosounders are like side-scan sonars: the higher the frequency, the more detailed the image and the narrower the swath. Unlike side-scan sonars, they have hundreds of transducers accurately recording echoes from discrete places on the seabed to collectively generate swath coverage (Fig. 1.5). This provides *xy* coordinates for the echoes so the time delay can be used to define *z* (depth). In this way, multibeam echosounders not only produce backscatter maps, like side-scan sonars, but also bathymetry. Multibeam echosounders have become essential tools to map cold-water coral reefs and coral carbonate mounds.

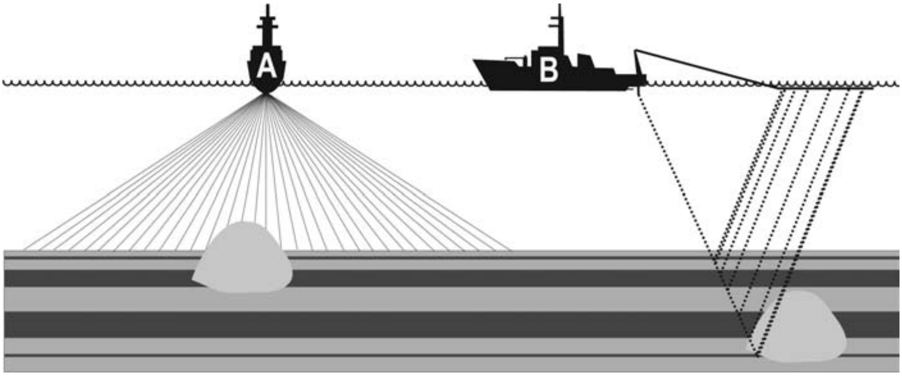

Fig. 1.5 Imaging a coral carbonate mound with sound. (a) Multibeam echosounders record a large number of discrete echoes from a swath of seabed thereby visualising seabed topography. Both the sound sources and receivers are hull-mounted. (b) Seismic imaging uses sound sources emitted near the vessel and received by a streamer towed behind. Low-frequency and high-magnitude sound sources penetrate the seabed and reflect off density contrasts (usually sediment unit boundaries and potentially buried coral carbonate mounds).

underwater vehicles (AUV) (e.g. Grasmueck *et al.*, 2006). Visual surveys are then performed using deep-towed camera frames although submersible or ROV-camera surveys are increasingly important (Colour plate 4). Submersibles and ROVs have the distinct advantages of being able to stop, wait, observe and take samples. They also allow monitoring equipment to be placed within specific macrohabitats or targeted at specific organisms. This opens new possibilities in experimental design where the organisms and habitats can be studied *in situ*. In this book we aim to capture the results of this revolution in cold-water coral research and note that in many instances this work has only just begun.

1.2.1 Exploration

The discovery of new cold-water coral reefs and mounds traces back to three primary sources: (1) chance finds and reports, often from fishing records, (2) sub-seabed seismic imaging data from frontier hydrocarbon exploration and (3) baseline regional mapping exercises.

The demand for oil and gas has made it profitable, and in some cases nationally strategic, to search for hydrocarbons with greater intensity and in deeper waters. So-called 'industrial seismics' use loud, low-frequency acoustic pulses (10 to 50 Hz) to penetrate deep into seabed rock strata to regions below the seafloor where hydrocarbon reservoirs might exist (see Topic box 1.1). Unfortunately, while low frequencies give good penetration through the seabed, they produce low-resolution datasets. On industrial seismic records, surface reefs are not visible but the more topographically expressive coral carbonate mounds, and some buried coral carbonate mounds, can be seen. In many instances, such seismic data have been detailed enough to identify mound targets for subsequent, higher resolution surveys. If hydrocarbon prospects are promising, then a closely spaced grid of seismic data (3D seismics) may be collected with interpolation between lines allowing a three-dimensional virtual seafloor to sub-seafloor block to be constructed. Buried coral carbonate mounds in the upper layers of seabed strata can be clearly imaged using this approach (Huvenne *et al.*, 2007).

Once governments started to exert control over their Exclusive Economic Zones (EEZs) and seafloor territories it became necessary to map them in greater detail. To map large areas of seabed one needs a wide coverage, or swath, of the seabed. Once again there is a trade-off, but this time the trade-off is between frequency, height above the seabed and swath. To achieve a wide swath, there needs to be a longer time between sonar pings and the sonar transducers need to be flown high enough above the seabed to allow the sound to spread out. The pioneering GLORIA long-range side-scan sonar operated at 100 kHz and made the first maps of many hundreds of thousands of square kilometres of seabed around the world in the 1970s and 1980s (Somers, 1996). It is now superseded by the 30 kHz TOBI system. Many discoveries were made with GLORIA including major features such as unknown submarine canyons and seamounts as well as extensive areas of coral carbonate mounds. The coral mounds on the Blake Plateau, northwest Atlantic and Irish margin were first mapped in this way. The relatively recent development of multibeam echosounders (see Topic box 1.1) has seen another revolution with each sounding being precisely positioned (an ambiguous shortfall with side-scan sonar systems) and the great additional benefit of accurate bathymetric as well as backscatter data (Colour plates 5, 15, 16).

1.2.2 Habitat mapping

To plan detailed sampling operations and map habitat it is necessary to have sufficiently resolved site maps at a scale that shows the heterogeneity of features such as cold-water coral reef or mound surfaces. This requires multibeam echosounders (~100 kHz) and higher frequency side-scan sonars (100–1000 kHz). In shallow water, multibeam echosounders can be hull mounted and side-scan sonars towed near the surface. In deeper shelf and slope waters, lower frequencies (e.g. 12 kHz) are required, resolution drops and it becomes more desirable to deploy the transducers nearer to the seabed. This can be done by deep-towing side-scan sonars but the more motion-sensitive multibeam echosounders need to be mounted on a stable near-seabed vehicle, such as an AUV or ROV, rather than being towed. This latter approach is now producing some exquisite images of the seafloor in deep water with a level of detail never seen before (e.g. Fig. 4.17, Colour plate 15).

However, sonar images are no more than typologies with changes in backscatter intensity. To interpret and add detail the seabed must be examined visually or sampled. This 'ground-truthing' can be done with camera systems or by collecting physical samples (see Section 1.2.3 below). As visible light travels a short distance through water any images will show at most only a few square metres of seabed. An array of imaging systems are now available from drop, towed and submersible-mounted camera systems to towed laser line scanners. Images from seafloor surveys can be 'stitched together' to make video-mosaics of the survey area (Fig. 4.3).

It is not possible, or environmentally advisable, to sample every portion of a seabed survey area. However, acoustic ground discrimination system (AGDS) techniques can be used to analyse the acoustic return from echosounders or side-scan sonar data (e.g. Fosså *et al.*, 2005). This AGDS software divides the coverage into areas of seabed with similar acoustic return signals (not just the echo intensity but also its delay or how the echo fades – whether the echo is short and crisp or with a more complex, longer return). These areas are termed acoustic facies. By ground-truthing each acoustic facies it is possible to use this information to characterise the nature of the seabed across the whole survey.

This diverse collection of spatial information can be collated, organised and visualised with geographical information system (GIS) software. This software stores and visualises digital spatial data allowing different datasets to be quickly added or removed to make custom maps and views that can then easily be displayed using different scales and mapping projections. Furthermore, the information can also be examined statistically to define and manipulate spatial relationships. Geographical information system outputs can include remotely sensed data, species occurrences, survey cruise tracks and interpreted habitat maps in any combination (Wright *et al*., 2007).

1.2.3 Collecting samples

As well as providing samples for ground-truthing geophysical surveys, physical samples from the deep seabed are vital for further study. A range of deep-water sampling approaches exist (see Gage & Tyler, 1991) but not all sample cold-water coral habitats effectively, especially scleractinian reefs where substrata contain hard coral frameworks and may even be lithified. Dredges and trawls were the mainstay of deep-sea sampling in the nineteenth and most of the twentieth centuries but there is now a consensus that they should be avoided in cold-water coral habitats. Not only do these devices group organisms from a range of habitats and facies altogether, but they are also very destructive. Hydraulically damped multi- and megacorers designed to delicately sample the sediment–water interface are often inappropriate in cold-water coral habitats where coral fragments or glacial dropstones prevent cores from penetrating. Large box corers (Fig. 1.6a) penetrate with greater force and collect relatively large (up to 0.25 m^2) samples with almost intact benthic assemblages. However, fine sediment material and meiofauna are often blown away by the corer's bow

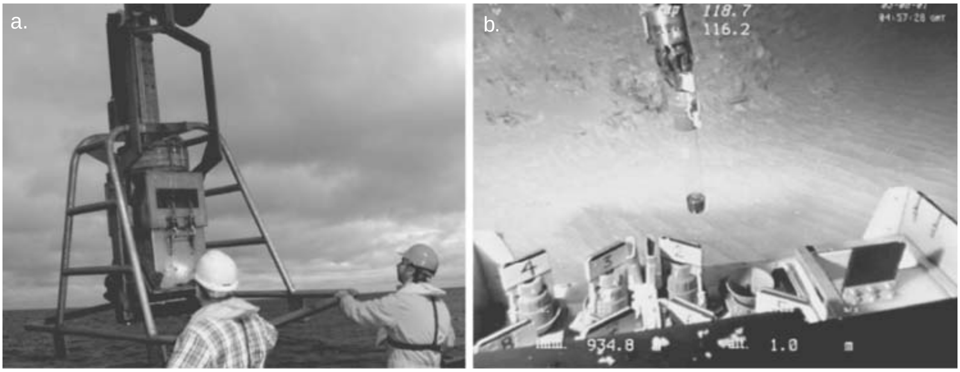

Fig. 1.6 A box corer (a) can recover up to 0.25 m^2 sediment surface area but is usually deployed without video guidance. Remotely operated vehicle push-cores (b) recover small sediment samples in a very precisely controlled manner. Image (b) courtesy of Ifremer (Institute Français de Recherche pour l'Exploitation de la Mer), Caracole Expedition 2001.

Fig. 1.7 A Russian hydraulically operated, video-directed seabed grab recovering a bottom sample from a coral carbonate mound in the Porcupine Seabight.

wave and rocks or coral fragments often prevent the corers from sealing properly. Intact box core samples are usually sub-sampled to separate surface and progressively deeper sub-surface layers and then sieved to separate species by size. Because box cores relate to area of seabed, quantified species diversity and biomass assessments can be made from intact cores. Submersibles and ROVs can sample specific habitats by either collecting selected organisms with manipulator arms or suction tubes (Colour plate 4), or by using push-cores forced into the seabed by a submersible/ROV manipulator arm (Fig. 1.6b). Recent developments in video-directed, hydraulically controlled grab sampling may allow coral colonies and reef frameworks to be sampled and stored in a sealed grab so that attached fauna are not lost as the sample is brought back through the water column (Fig. 1.7).

Continuous marine seabed deposition offers several advantages over what are typically more disrupted terrestrial records making long seabed cores valuable archives of past environmental conditions. Hemipelagic sedimentary sequences, despite low sedimentation rates, are relatively soft and easy to core with gravity or piston cores. Coral carbonate mounds have higher accumulation rates (see Section 4.4.3, p. 127) and may provide higher resolution archives, although complex sedimentation processes may restrict interpretations. The high carbonate content of these mounds provides valuable environmental proxies (coral skeletal proxies are discussed in Chapter 7). However, coral frameworks and lithification produce hard substrata that inhibit conventional coring and can bend core barrels (Fig. 1.4). This means that access to long core sequences can only be achieved effectively with drilling techniques, especially if whole mound sequences are to be sampled. Examples include drill ships like the *RV Joides Resolution* or portable deployable drilling rigs such as *MeBo* (Meeresboden-Bohrgerät; Freudenthal & Wefer (2007), see Fig. 1.8). With these devices, complete

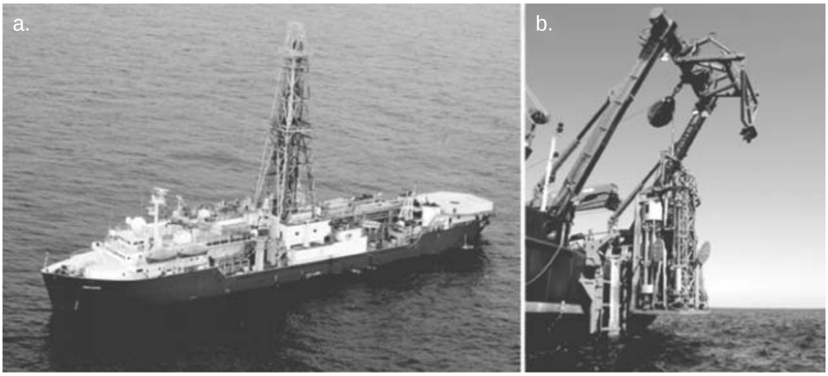

Fig. 1.8 Drilling technologies. (a) The 143 m long Integrated Ocean Drilling Program (IODP) drill ship *RV Joides Resolution* is capable of drilling up to 2000 m below the seafloor in water depths up to 8000 m. Image courtesy of the Integrated Ocean Drilling Program. (b) The German *Meeresboden-Bohrgerät* (seafloor drill rig) known as *MeBo* deployed from the stern of a research vessel. This portable system is designed to drill 50–70 m below the seafloor in water depths up to 2000 m. Image courtesy of MARUM, University of Bremen, Germany.

sequences tens of metres long can be retrieved through both soft and lithified substrata. However, the costs of these drilling approaches are substantial.

1.2.4 Monitoring

Acoustic maps and samples provide ‘snapshots’ of a dynamic environment. Cold-water coral habitats are strongly influenced by fast-flowing currents that flush through them. Seasonal changes affect surface productivity, which in deep-sea settings leads to seasonal changes in phytodetrital flux to the seafloor. Our snapshots of these environments are usually during spring or summer months when calmer seas make surveys possible. However, mobile sedimentary bedforms may take several years to migrate through areas where cold-water corals are present and we are just starting to appreciate decadal changes in deep-sea climate conditions.

Continuous monitoring in the deep sea can overcome this temporal sampling bias and offer us a different view of these environments – revealing periods of change, the variability of environmental conditions and possibly even infrequent, but important, extreme events. Monitoring can be done by deploying instrumented platforms (such as benthic landers, Fig. 1.9) on the seabed or moorings with strings of instruments monitoring processes in the water column. Typical instrument packages include both single-point current meters and acoustic doppler current profilers, sediment traps, fluorometers to record phytoplankton pigments, light-scattering and transmission sensors to record particle resuspension, and time-lapse cameras to monitor organism presence and activity.

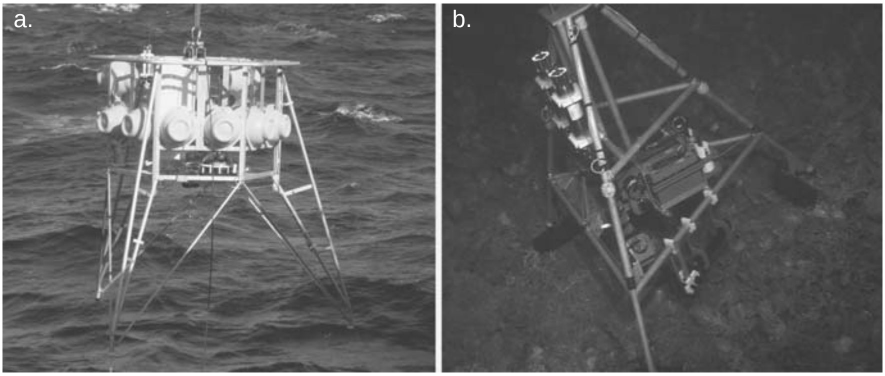

Fig. 1.9 Benthic landers allow cold-water coral habitats to be monitored through time. (a) The Royal Netherlands Institute for Sea Research BoBo lander being deployed on the Logachev Mounds, northeast Atlantic and (b) the Scottish Association of Marine Science photolander on the Galway Mound (800 m depth), northeast Atlantic. Image (a) courtesy of B. Dorschel and image (b) courtesy of the Alfred-Wegener-Institut für Polar- und Meeresforschung and the Institut Français de Recherche pour l'Exploitation de la Mer.

1.2.5 Technologies for the future

Submersibles and ROVs have already revolutionised how we interact with deep, cold-water coral environments; not only do they enable a flexible presence on the seabed, but with the development of different tools and payloads they can operate in various modes from reconnaissance and mapping to observation and sampling. Increasingly, ROVs are being used as workhorses to accurately position, maintain and retrieve experiments from the seabed. These can examine a suite of topics including animal behaviour, physiology, reproduction and larval settlement all ideally related back to long-term *in situ* monitoring information from benthic landers and moorings.

Other technologies are now being developed to the point where they can be used to study deep-sea habitats. With increasing payload capacities, AUV-based surveying is destined to become increasingly important. Autonomous underwater vehicles offer new opportunities allowing systematic surveys such as seabed mapping or water mass characterisation leaving the AUV's mother ship and scientists free to perform other activities. Benthic crawlers are now being developed to explore spatial variability in the deep sea. Rather like the Mars rovers, crawlers are small motorised machines that can drive over the seabed carrying a payload of instruments and cameras. A crawler could be remotely controlled, pre-programmed or even able to 'intelligently' explore the environment and find its way back to a docking station to recharge its batteries and download its data. This new tool may be able to explore and sample cold-water coral habitats where other tethered vehicles are constrained by fast currents.

Cabled observatories perhaps offer the greatest potential for the next revolution in the way researchers interact and study cold-water coral habitats. Cabled observatories create a real-time permanent presence in these remote environments using fibre-optic cables to relay information straight back to shore and, via the World Wide Web, to researchers around the world (Delaney & Chave, 2000). Observatories can be considered as hard-wired lander platforms and moorings but without the power and payload constraints of autonomous systems they can be much larger and more sophisticated. Cabled observatories could also monitor internal reef and mound environments, connecting down-borehole probes measuring sub-seafloor processes such as fluid flow.

Seafloor observatory nodes could also become energy supply and data download stations for AUVs and crawlers allowing them to remain deployed for prolonged periods. At the time of writing North American cabled observatory plans are being implemented in the North Pacific (the MARS, NEPTUNE and VENUS projects). In Europe plans have been laid for an observatory including coral carbonate mounds in the Porcupine Seabight (ESONET). Seafloor observatories have the potential to bring these remote environments directly into the laboratory, classroom or home in real time. Such technologies will surely change how we perceive and study these environments and initiate a new era in deep-sea exploration.

2

Cold-water corals

> *It is temperature rather than depth that controls the bathymetric distribution of all corals except the shallow-water forms . . .*
>
> Ecology of modern marine organisms with reference to paleogeography
> Thomas Wayland Vaughan (1940)

What is a coral? Dictionary definitions vary, probably because the concept of the word coral is not a scientific one, but rather a layman's term. Like the omnibus words 'bug' and 'worm', these words mean different things to different people and professions. In all three cases, these words refer to a polyphyletic assemblage of organisms, not a natural unit of evolution. Nonetheless, over the last century the term coral has come to refer to seven cnidarian taxa that have been defined by Cairns (2007, p. 312) as: 'Animals in the cnidarian classes Anthozoa and Hydrozoa that produce either calcium carbonate (aragonitic or calcitic) secretions resulting in a continuous skeleton or as numerous microscopic, individualised sclerites, or that have a black, horn-like, proteinaceous axis.' This is admittedly a cumbersome definition, but is necessarily so in order to include the seven disparate coral taxa, which are listed in Table 2.1. This classification table also gives some common names used for all or part of these seven taxa, as well as the current number of valid Recent species. From this table we see that as of early 2007, there were approximately 5160 species of corals, 65% of which occur in water deeper than 50 m. Thus, corals are not the shallow-water phenomena that many associate with the name, but corals are primarily deep, cold-water inhabitants. Five of the seven taxa (those in bold in Table 2.1) have a high percentage of species that occur in deep, cold waters; these taxa will be discussed in more detail below. For a recent wider review of phylogenetic patterns in the Cnidaria see Daly *et al.* (2007).

2.1 Ecological categorisation of corals

In order to better define the distinction between deep-water and shallow-water corals, Wells (1933, p. 109) proposed the terms hermatypic and ahermatypic, the former

Table 2.1 *Classification of the seven different coral groups with some common names, the total number of species (as of March 2007) and number of deep-water (>50 m) species (modified after Cairns, 2007). Taxa in bold are discussed in the text. (*implies an estimate)*

Taxon	Common names	Number species	Number species deeper than 50 m
Phylum Cnidaria (= Coelenterata)			
Class Anthozoa			
Subclass Hexacorallia (= Zoantharia)			
Order **Scleractinia** (= Madreporaria)	hard corals, stony corals, true corals, cup corals, star corals, solitary corals, zooxanthellate corals, azooxanthellate corals	1488	622
Order **Zoanthidea** (in part)	zoanthids, gold coral (*Gerardia* spp.)	3	3
Order **Antipatharia**	black corals, whip corals, wire corals, thorny corals	*241	*182
Subclass **Octocorallia** (= Alcyonaria)	soft corals, gorgonians, sea fans, sea whips, sea feathers, precious corals, pink coral, red coral, golden corals, bamboo corals, leather corals, horny corals, sea pens	*3159	*2325
Class Hydrozoa			
Subclass Hydroidolina			
Order Anthoathecata (= Athecata)	athecate hydroids		
Suborder Filifera			
Family **Stylasteridae**	‘hydrocorals’, lace corals, stylasterids	249	223
Family Hydractiniidae (in part)	longhorn hydrozoans (*Janaria, Hydrocorella*)	3	1
Suborder Capitata			
Family Milleporidae	‘hydrocorals’, fire corals, millepores	17	0
Total		*5160	*3356

referring to reef-building corals that possess zooxanthellae in their tissue, the latter to those corals that do not form shallow-water reefs and lack zooxanthellae. Unfortunately, nature cannot be so easily partitioned, in that there are shallow-water reef-building corals that lack zooxanthellae, and zooxanthellate corals that do not contribute to reef structure and, of course, there are cold-water, reef-framework structures composed of azooxanthellate species that are a focus of this book. Thus, the terms hermatypic and ahermatypic, and reef and non-reef were used in a variety of ways by both biologists and geologists, the history well summarised by Schuhmacher and Zibrowius (1985). Ultimately, Schuhmacher and Zibrowius (1985, p. 3) and Zibrowius (1989) applied an ecologically tripartite classification to scleractinian corals, every species classified as being zooxanthellate or azooxanthellate, hermatypic or ahermatypic, and constructional or non-constructional, an ecological classification that can be applied to non-scleractinian corals as well. The first set of terms is self-evident, but Schuhmacher and Zibrowius defined a hermatypic coral as one that contributed to the framework of a reef, and went on to define a reef as ‘a persistent, positive topographic biogen structure, rising up to the surface of the sea and characterised by its capability to resist hydrodynamic stress’. In other words, a reef had to be a shallow-water structure in the classic sense of the word, i.e. ‘a structure lying at or near the surface of the water’ (Oxford English Dictionary), but in this book we extend the definition of reef to include deep-water framework-forming corals (see Topic box 2.1). Conversely, ahermatypic species do not contribute significantly to shallow-water reef structure, which is sometimes a subjective call. To further categorise deep-water, reef-framework structures, Schuhmacher and Zibrowius coined the terms constructional and non-constructional; constructional (sometimes called habitat-forming and structure-forming) species being those that contribute to an elevated, durable, carbonate structure, either in deep or shallow water. We have reorganised their categories into a graphic, annotated flow chart (Fig. 2.1). But, we have slightly modified their classification to allow some ahermatypic corals to be categorised as deep-water reef framework-formers (Topic box 2.1).

Among the 711 valid azooxanthellate scleractinian species (see Online Appendix at www.lophelia.org/coldwatercoralsbook), virtually all are non-constructional, ahermatypic species, whereas only 18 are constructional (Fig. 2.1, Table 2.1). The latter small group are the kinds of species that will be most discussed in this book. Of those 18, most (17) occur in deep water and are thus ahermatypic constructional species, and only one, *Tubastraea micranthus*, is a shallow-water hermatypic constructional species. Of the 777 zooxanthellate species, 767 are constructional, and most of those hermatypic in the sense that they contribute to shallow-water reef structure. A very few zooxanthellate species form structures in slightly deeper water, the ahermatypic constructional zooxanthellates. Of these 10 to 15 species are zooxanthellate, non-constructional, ahermatypic species, in

Topic box 2.1 **What makes a reef?**

The word reef derives from the Old Norse seafaring term ‘rif’ – a submerged structure rising from the surrounding seafloor shallow enough to endanger ships. Such structures could be rock ridges, sandbanks or coral reefs – classically defined as the substantial accumulations of limestone formed by a framework of coral skeletons often cemented by coralline algae in shallow-water tropical seas (Wood, 1999). But can cold-water corals form reefs?

Biogenic reefs form self-sustaining patches as the skeletal remains of the reef organisms themselves form hard substrata rising from the seafloor. These reefs are created by various organisms including the tubes of serpulid polychaete worms such as *Serpula vermicularis* (Bosence, 1979), the siliceous skeletons of hexactinellid sponges (Conway *et al*., 2005) and the limestone skeletons of scleractinian corals (Birkeland, 1997). Biogenic reef growth is balanced by the (bio)erosive processes that tend to break the reef framework structure down. If growth exceeds (bio)erosion, biogenic reefs can grow large enough to alter hydrodynamic and sedimentary conditions and form structurally complex habitat for other species. They are long-lived, a feature that may help explain the evolution of complex and intricate symbiotic relationships between many reef inhabitants.

This book describes cold-water corals not just in terms of their biology but in terms of the habitats they form and their geological significance. Naturalists have known that corals could form local ‘banks’ or ‘hills’ in cold, deep waters since the days of Linnaeus but only recently have we realised the scale of cold-water coral habitats and begun to study how they function. It is becoming clear that the structural habitats formed by the major framework-forming scleractinian corals described in this chapter fulfil the key ecological and geological definitions of a reef; they are long-lived, their growth is balanced by (bio)erosion, they form local topographic highs that alter hydrodynamic and sedimentary regimes, and they form structural habitat for many other species including specialised symbioses that are now being examined for the first time. Other cold-water coral habitats, such as assemblages of deep-water gorgonians that do not form long-lived skeletal frameworks, cannot be considered to form reefs.

However, scleractinian reef framework-forming cold-water corals grow in waters too deep to endanger shipping – and by the dictionary definition therefore cannot be said to form reefs. But the term reef is no longer restricted to nautical use. In this book we summarise and review the growing evidence that cold-water corals can form biogenic reef frameworks, in the geological and ecological senses. As well as the scientific criteria outlined here, reef is also a term used by governments in marine conservation legislation (see Chapter 8 and discussion in Case study 8.2, p. 242). We believe that depth of occurrence is too simplistic a reason to prevent cold-water scleractinian corals being thought of as reef framework-forming. Whether these frameworks can be considered to develop reefs per se depends on the scale on which one is operating and the particular reef framework under consideration. The criterion

Topic box 2.1 (cont.)

that a reef should locally trap sediment is particularly important here. For the purposes of this book, we will define those scleractinian corals whose colonies form complex three-dimensional structures as *reef framework-forming* and further refine the ecological categorisation of corals by developing the terminology discussed by Schuhmacher and Zibrowius (1985), see Section 2.1, p. 20.

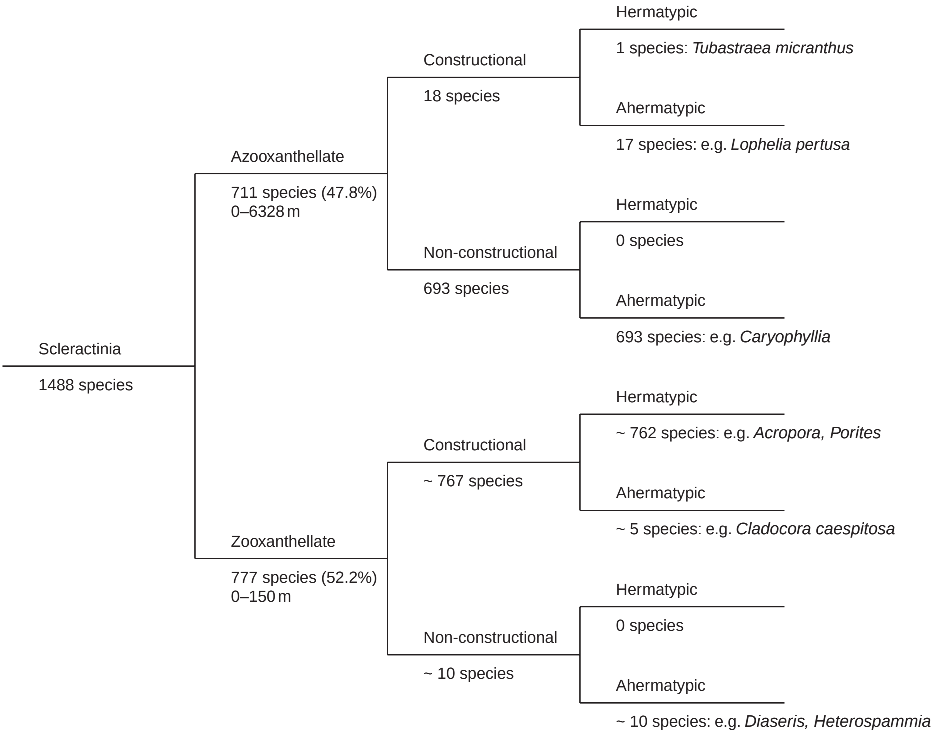

Fig. 2.1 The six ecological permutations of scleractinian corals, the number of species/groups and some examples.

that, although they have zooxanthellae, they are either too small, of a solitary growth form or occur in such isolated patches that they do not contribute significantly to shallow-water reef structure.

2.2 The five cold-water coral taxa

Another way to categorise cold-water corals is as habitat-forming organisms and these species are the emphasis in this book. From the earliest naturalists' reports, many have noted that the structural complexity of cold-water corals provides habitat and refuge

Table 2.2 *Recent azooxanthellate Scleractinia.*

Family	Number of genera	Number of species	Number of species deeper than 50 m
Caryophylliidae	43	294	269
Dendrophylliidae	18	152	118
Flabellidae	10	98	96
Turbinoliidae	23	57	56
Rhizangiidae	4	32	9
Fungiacyathidae	1	20	20
Oculinidae	6	14	12
Micrabaciidae	4	13	13
Pocilloporidae	1	8	7
Anthemiphylliidae	1	7	7
Gardineriidae	2	6	6
Stenocyathidae	3	3	3
Schizocyathidae	3	3	3
Guyniidae	1	1	1
Incertae Sedis	–	3	2
Total	**120**	**711**	**622**

for many associated species and we consider these ecological aspects in Chapter 5. Here we will consider those cnidarian taxa that contribute significantly to cold-water coral habitats by providing reef frameworks or other structural habitat.

2.2.1 Scleractinia

Six hundred and twenty-two of the 711 azooxanthellate scleractinian species occur in water deeper than 50 m; the remaining 89 azooxanthellate species are confined to shallow water (Table 2.2). Deep-water azooxanthellates are ubiquitous in marine waters, occurring from off continental Antarctica to the Barents Sea (71°21′N), well within the Arctic Circle, absent only from the Bering Sea and high Arctic regions. They occur in temperatures as low as −1.1°C (Vaughan & Wells, 1943, p. 353), and to depths of 6328 m in the Aleutian Trench (Keller, 1976). Their realm far exceeds that of their zooxanthellate counterparts (Cairns & Stanley, 1982). Whereas some species occur at great depths, most live on continental slopes between 200–1000 m, the same depths at which most of the cold-water coral reefs and mounds occur. Contrary to popular belief, not all cold-water scleractinian corals are 'solitary' corals, fully 26% being colonial (Cairns, 2007), this latter group containing all the larger, framework-forming species discussed below. Furthermore, not all cold-water scleractinian corals are firmly attached to the substratum, as are most shallow-water reef corals; whereas 53% are attached, 37% are unattached and another 9% experience transverse division, resulting in an unattached corallum (an anthocyathus) from an attached base (an anthocaulus) (Cairns, 2007). Taxonomically, cold-water scleractinian corals occur in 14 scleractinian families (Table 2.2) and 114 genera, by far the most species belonging to the family Caryophylliidae, to which most of the structure-forming species belong (Table 2.2). Although rarely of commercial value, geochemical studies of deep-water scleractinians have provided useful information for palaeoceanography, see Chapter 7.

A brief history of taxonomic research on cold-water scleractinian corals was published by Cairns (2001a), which included a graph of the cumulative number of described species since 1758, and a discussion of the significant coral taxonomists to date (see Chapter 1, Section 1.1.1, p. 2). All species are listed by Cairns *et al*. (1999) and updated in the Online Appendix (www.lophelia.org/coldwatercoralsbook), the latter of which includes for the first time junior synonyms and depth ranges for all species. Keys to deep-water Scleractinia are few and far between, perhaps because it is inadvisable and misleading to create keys to a fauna that is so poorly known, and because there have been so few deep-sea coral taxonomists. Vaughan and Wells (1943) contains keys to all species known at that time, whereas all other keys are regional in nature: northeast Atlantic (Cairns, 1981); southeastern Australia and Tasmania (Cairns & Parker, 1992); northeastern temperate Pacific (Cairns, 1994); and the Brazilian coast (Kitahara, 2007). Most of the higher taxa of cold-water corals are listed and illustrated on the Tree of Life web project: http://tolweb.org/Scleractinia.

As mentioned above, there are 17 known species of deep, cold-water, framework-forming (and thus habitat-forming) scleractinians (Table 2.3), only six of which are considered to be widespread and thus of more significance (indicated in bold type below). These species are rarely more than two metres in height and bushy in habit, producing three-dimensional reef frameworks that provide habitat for a great diversity of fish and other invertebrates, as well as surfaces for settlement by solitary corals. These deep, cold-water reef habitats are discussed more fully in Section 5.1.1, p. 145.

Lophelia pertusa (Fig. 2.2) is the most common reef framework-forming cold-water coral. It forms bush-like colonies that may grow to be several metres across consisting of thousands of coral polyps. As the colony develops, adjacent branches can anastomose, considerably strengthening the reef framework. Although sometimes referred to as the ‘white coral’, *L. pertusa* also occurs in yellow, orange or red variations of the generally translucent tissue. This coral has been found most frequently in the North Atlantic but has a cosmopolitan distribution (Zibrowius, 1980) occurring throughout the Atlantic, taking in parts of the Mediterranean Sea, the Gulf of Mexico and the Caribbean Sea (Fig. 2.3). It is also known from a few locations in the Indian and Pacific Oceans (Zibrowius, 1973; Cairns, 1984).

A band of *L. pertusa* stretches from the southwestern Barents Sea along the eastern Atlantic continental margin down to West Africa. Although less well characterised

Table 2.3 *Framework-forming (constructional), azooxanthellate Scleractinia with the six most significant cold-water species in bold face (asterisk indicates shallow, i.e. hermatypic, species).*

Family Pocilloporidae
- *Madracis myriaster* (Milne Edwards & Haime, 1849)
- *M. interjecta* Marenzeller, 1907

Family Oculinidae
- ***Oculina varicosa* Lesueur, 1821**
- ***Madrepora oculata* Linnaeus, 1758**
- *M. carolina* Pourtalès, 1871

Family Caryophylliidae
- ***Lophelia pertusa* (Linnaeus, 1758)**
- ***Solenosmilia variabilis* Duncan, 1873**
- *Desmophyllum dianthus* (Ehrenberg, 1834)
- ***Goniocorella dumosa* (Alcock, 1902)**
- *Pourtalosmilia conferta* Cairns, 1978
- *Anomocora fecunda* (Pourtalès, 1871)
- *Coenosmilia arbuscula* Pourtalès, 1874
- *Cladocora debilis* Milne Edwards & Haime, 1849

Family Dendrophylliidae
- ***Enallopsammia profunda* (Pourtalès, 1867)**
- *E. rostrata* (Pourtalès, 1878)
- *Dendrophyllia alternata* Pourtalès, 1880
- *D. minuscula* Bourne, 1905
- *Tubastraea micranthus** (Ehrenberg, 1834)

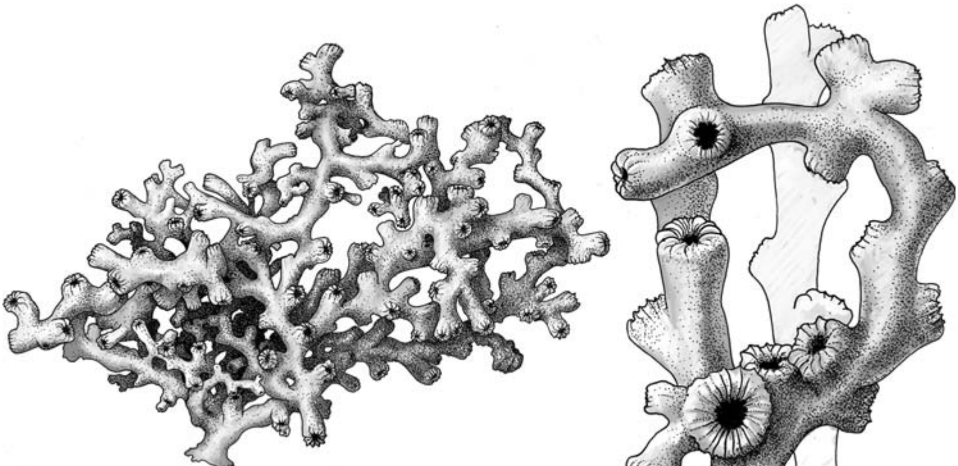

Fig. 2.2 Drawing of a *Lophelia pertusa* skeleton showing the framework formed by the coral colony and the details of individual polyp calices. Both scale bars 10 mm.

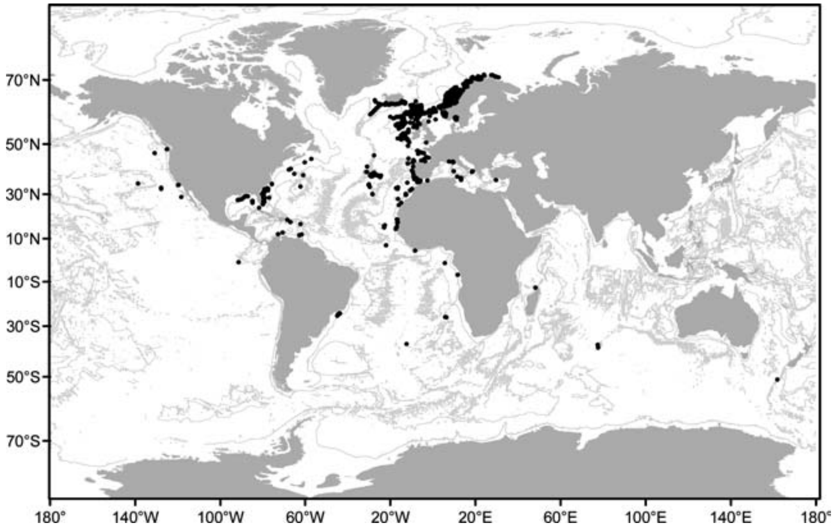

Fig. 2.3 Global distribution of *Lophelia pertusa* (isobaths at 2000 m, 5000 m and 9000 m depth).

at the time of writing, there is growing evidence of a similar band along the western margin of the Atlantic, from Nova Scotia to the Florida Straits and into the Gulf of Mexico. The northernmost *L. pertusa* occurrence known to date is from the south-western Barents Sea near Hjelmsøybank at 71°21′N, 24°00′E (Fosså *et al.*, 2000), while the southernmost location is on the sub-Antarctic Macquarie Ridge off New Zealand at 51°S, 162°01′E (Cairns, 1982). The shallowest occurrence of live *L. pertusa* has been recorded at just 39 m depth in Trondheimsfjord, mid-Norway (see Colour plates 6, 7, 8), and the deepest records are 3383 m from the New England Seamount chain and 2775 m off Morocco (Zibrowius, 1980).

In contrast to the monospecific genus *Lophelia*, the genus *Madrepora* contains several species and two of them, ***Madrepora oculata*** (Fig. 2.4) and *Madrepora carolina* are often associated with cold-water coral reefs. The branched colonies of *Madrepora* are generally far more fragile than those of *L. pertusa* limiting its framework-building capacity and thick reef frameworks do not develop where *Madrepora* dominates the coral community. *Madrepora* often co-occurs with more robust framework-forming species such as *L. pertusa* and *Goniocorella dumosa* where it can be thought of as a secondary framework-forming species.

Like *L. pertusa*, species of *Madrepora* are cosmopolitan (Fig. 2.5). In some areas of the northeast Atlantic and the Mediterranean Sea, *M. oculata* can dominate the coral community; in the western Atlantic, *M. oculata* overlaps with *M. carolina*. The northernmost record of *M. oculata* is from the Andfjord, northern Norway at 69°14′N, 16°41′E (Zibrowius, 1980), and the southernmost is from the sub-Antarctic Drake Passage at 59°49′S, 68°52′W (Cairns, 1982). The shallowest depths at which

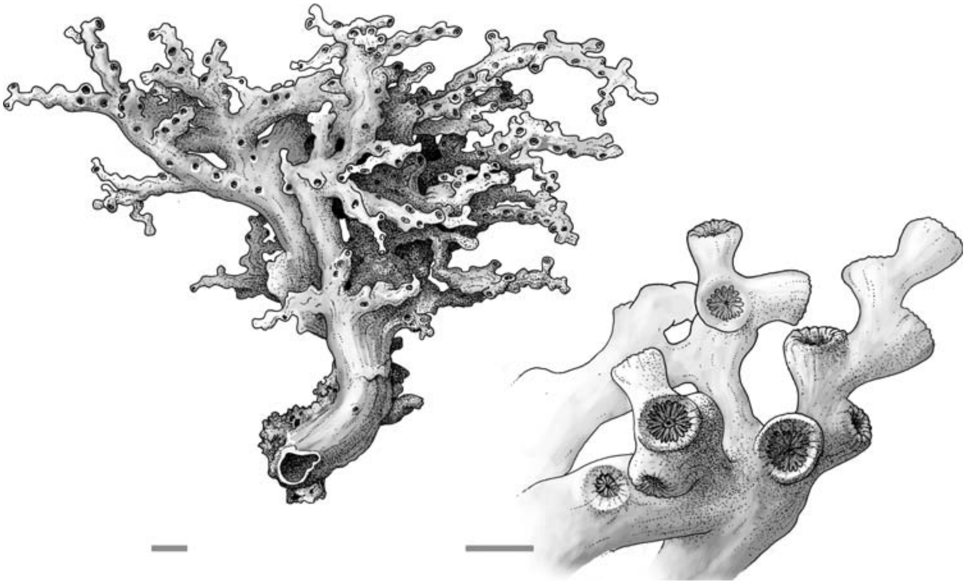

Fig. 2.4 Drawing of a *Madrepora oculata* skeleton showing the structure formed by the coral colony and the details of individual polyp calices. Note opening of a symbiotic eunicid polychaete tube at the base of the coral colony. Scale bars: 10 mm (coral colony) and 4 mm (calyx detail).

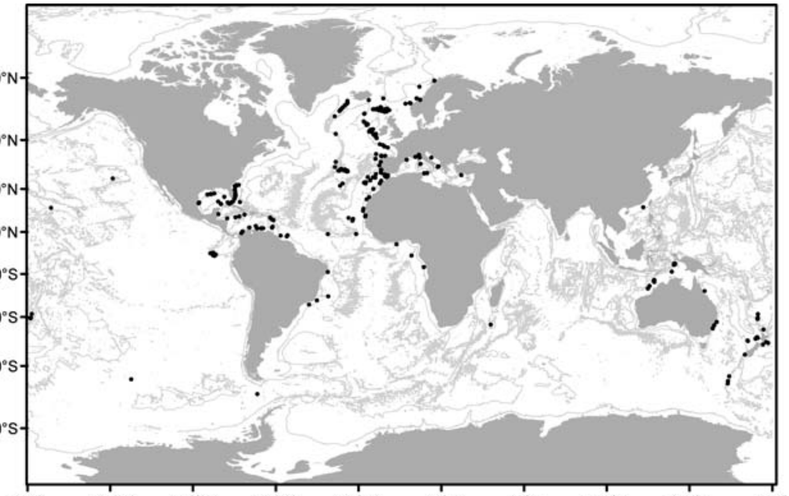

Fig. 2.5 Global distribution of *Madrepora oculata* (isobaths at 2000 m, 5000 m and 9000 m depth).

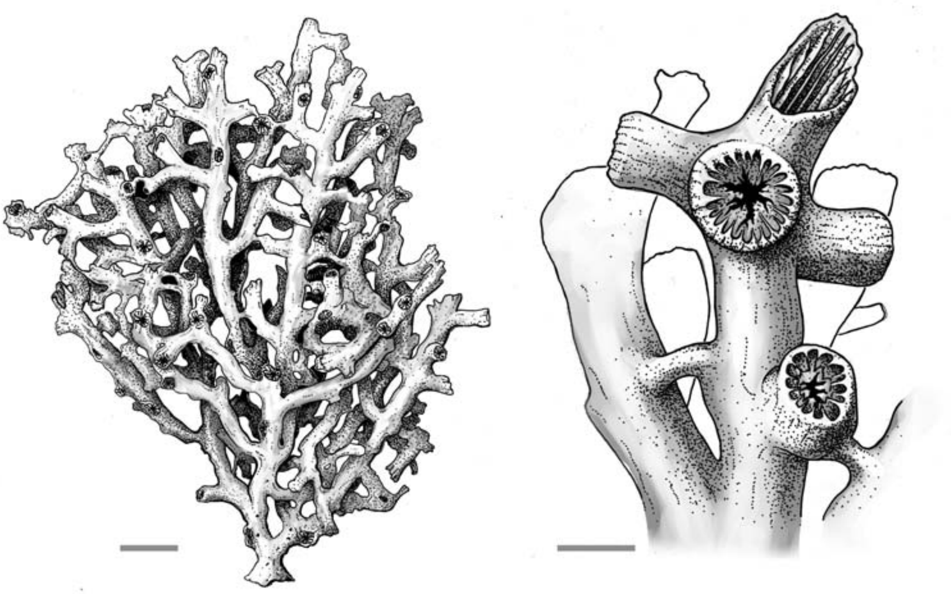

Fig. 2.6 Drawing of a *Goniocorella dumosa* skeleton showing the fragile framework formed by the coral colony and the details of individual polyp calices. Note the small bridges (coenosteal processes) between separate coral branches. Scale bars: 10 mm (coral colony) and 3 mm (calyx detail).

live *M. oculata* have been found are 55 m off Brazil and at 60–120 m in the mid-Norwegian Heltefjord; the deepest occurrences have been recorded from the southern Reykjanes Ridge at 1950 m and from 1694 m near the Cape Verde Islands (Zibrowius, 1980).

The biology of ***Goniocorella dumosa*** (Fig. 2.6) is poorly known. It is found primarily in the southern hemisphere (Fig. 2.7), mostly in New Zealand's waters and adjacent banks such as the Campbell Rise and Chatham Rise (Cairns, 1995). Elsewhere this coral has been recorded from South African, Indonesian and Korean waters. The known bathymetric range is from 88–1488 m with a concentration of records at depths of 300–400 m.

Oculina varicosa (Fig. 2.8) is found in shallow waters in the Caribbean Sea, Gulf of Mexico and Atlantic from Florida to North Carolina where it occurs with endosymbiotic zooxanthellae. In deeper waters this species can be azooxanthellate and develop reef frameworks between 3–35 m in height at depths of 45–100 m along the eastern Florida Shelf (Reed, 2002).

Of four valid species in this genus, ***Enallopsammia profunda*** (Fig. 2.9) is the major reef framework-forming species (Stetson *et al*., 1962; reported as *Dendrophyllia profunda*) capable of forming large dendroid colonies up to a metre

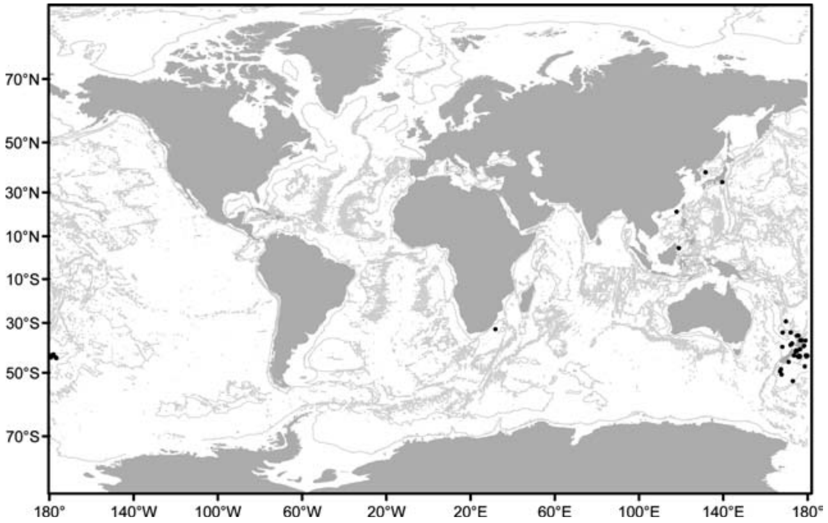

Fig. 2.7 Global distribution of *Goniocorella dumosa* (isobaths at 2000 m, 5000 m and 9000 m depth).

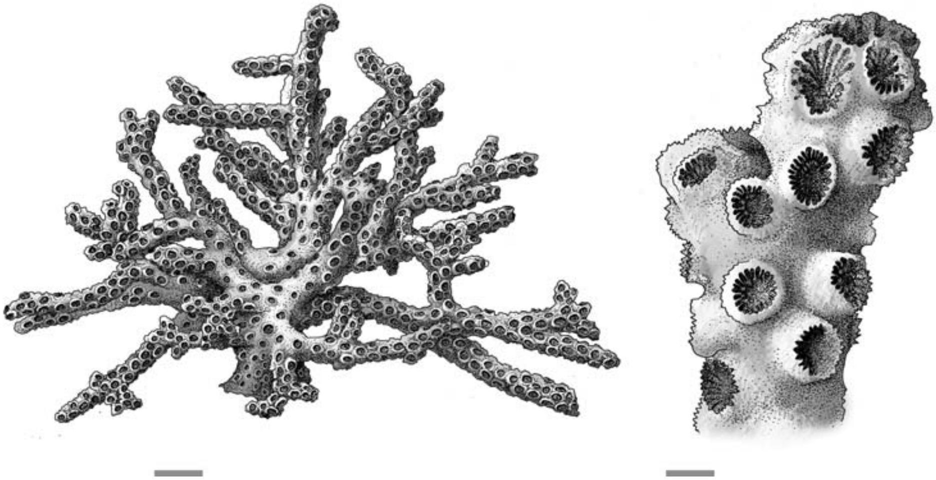

Fig. 2.8 Drawing of an *Oculina varicosa* skeleton showing the structure formed by the coral colony and the details of individual polyp calices. Scale bars: 10 mm (coral colony) and 3 mm (calyx detail).

thick. It is endemic to the western Atlantic and ranges from the Antilles in the Caribbean to off Massachusetts at depths from 403–1748 m (Cairns, 1979). It is often associated with *L. pertusa*, *M. oculata* and *Solenosmilia variabilis* (see Reed, 2002) and co-occurs with these species in coral banks on the outer eastern edge of the Blake Plateau off North Carolina at depths of 640–869 m. Other

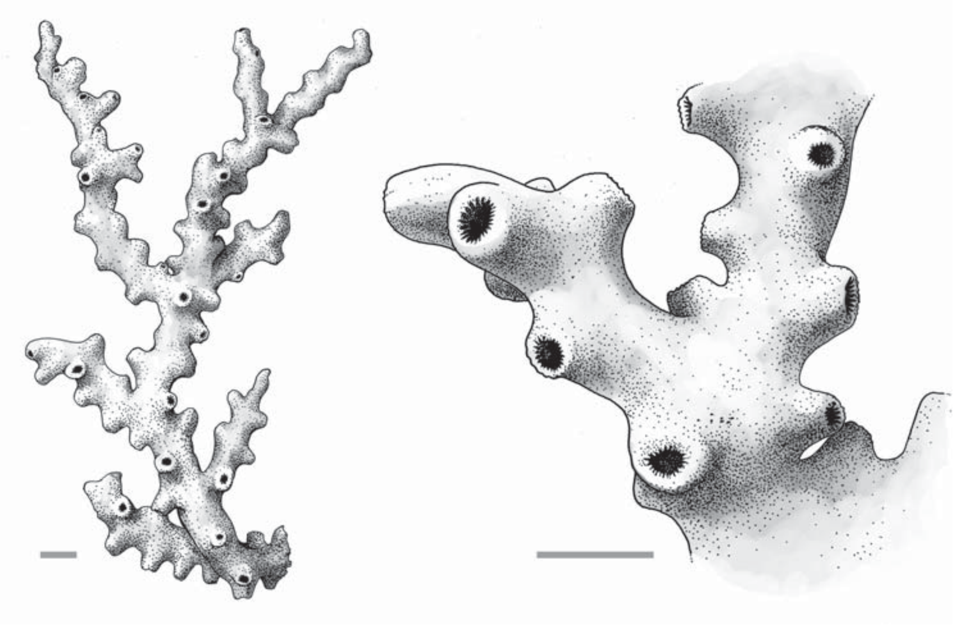

Fig. 2.9 Drawing of an *Enallopsammia profunda* skeleton showing the structure formed by the coral colony and the details of individual polyp calices. Both scale bars 10 mm.

occurrences are reported along the Florida-Hatteras Slope at similar depths where sizeable mounds of up to 100 m in height have been reported (Reed, 2002).

Solenosmilia variabilis (Fig. 2.10) has a generally cosmopolitan distribution (Fig. 2.11), but has not yet been recorded from the Antarctic or in the North or East Pacific (Cairns, 1995). It occurs between 220–2165 m water depth and is often associated with *L. pertusa*, *Madrepora* spp. and *E. profunda*. Dense aggregations of *S. variabilis* have been found on the summits of the South Tasmanian Seamounts in depths of 1000–1400 m. Bycatch reports indicate that it probably occurred to shallower depths of 600 m (Koslow *et al.*, 2001). Large quantities have been found in the Heezen Fracture Zone in the South Pacific and *Solenosmilia* also occurs in the Indian Ocean along the slopes of St. Paul and Amsterdam (Zibrowius, 1973). This species has also been found in the Atlantic from the northern slope of Little Bahama Bank at depths of 1000–1300 m (Mullins *et al.*, 1981) and from the Reykjanes Ridge, south of Iceland at depths of 1000–1900 m (Copley *et al.*, 1996).

2.2.2 Zoanthidae

Most of the approximately 200 species in the order Zoanthidea are soft-bodied creatures; only one genus in one family, *Gerardia* in the family Gerardiidae

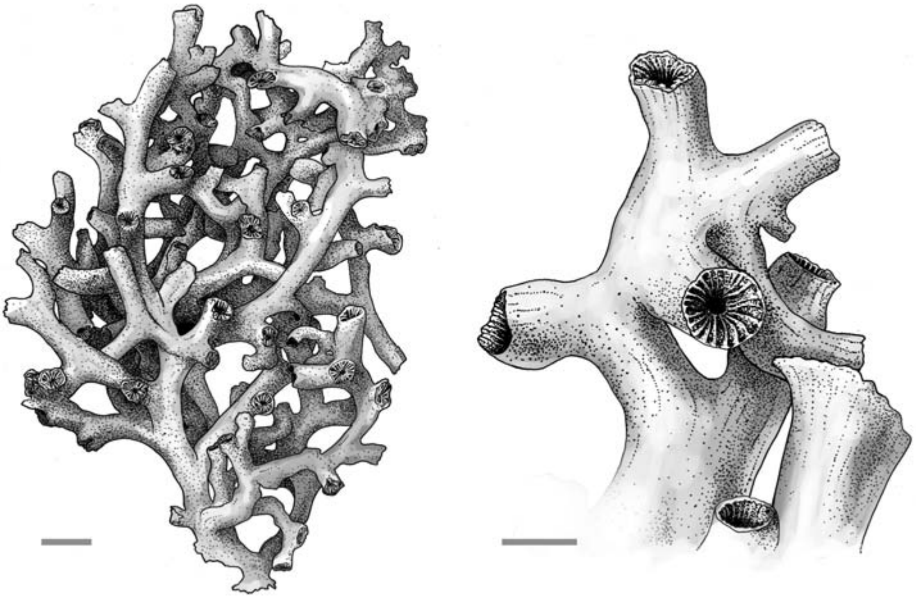

Fig. 2.10 Drawing of a *Solenosmilia variabilis* skeleton showing the framework formed by the coral colony and the details of individual polyp calices. Scale bars: 10 mm (coral colony) and 3 mm (calyx detail).

(Colour plate 9), forms a dense, gold-coloured, layered proteinaceous axis or encrustation. *Gerardia* contains only three species, all occurring in deep water: two are known from the North Atlantic and one from the central Pacific. The most current taxonomy of this group is that of Ocaña and Brito (2004). The species that occurs in abundance in the central Pacific, and is common in the Hawaiian archipelago and Emperor Seamount Chain (Parrish & Baco, 2007) at depths of 350–600 m, has not yet been named, and was previously referred to as *Parazoanthus* sp. (e.g. Grigg, 1974) or more recently simply as *Gerardia* sp. *Gerardia* is one of the longest-lived animals yet observed in the ocean. Druffel *et al*. (1995) assigned an age of 1800 years to Bahamian specimens, which they likened to the '*bristlecone pines of the deep-sea*'. With such a long life and hard skeleton, *Gerardia* has great potential as an archive of changes in oceanic productivity and particle flux (Druffel *et al*., 1995), see Section 3.4.2, p. 91.

The skeleton of *Gerardia* is also used in the Hawaiian jewellery industry, much in the same ways as *Corallium* (Grigg, 2002), see Section 8.1.5, p. 251. Hawaiian *Gerardia* occurs as large golden-yellow colonies up to 3 m in both height and width (Colour plate 9), and often encrusts the axes of other benthic cnidarians (Parrish & Baco, 2007), but at other times appears to form independent branched colonies. They are flabellate in shape, the plane of the colony oriented

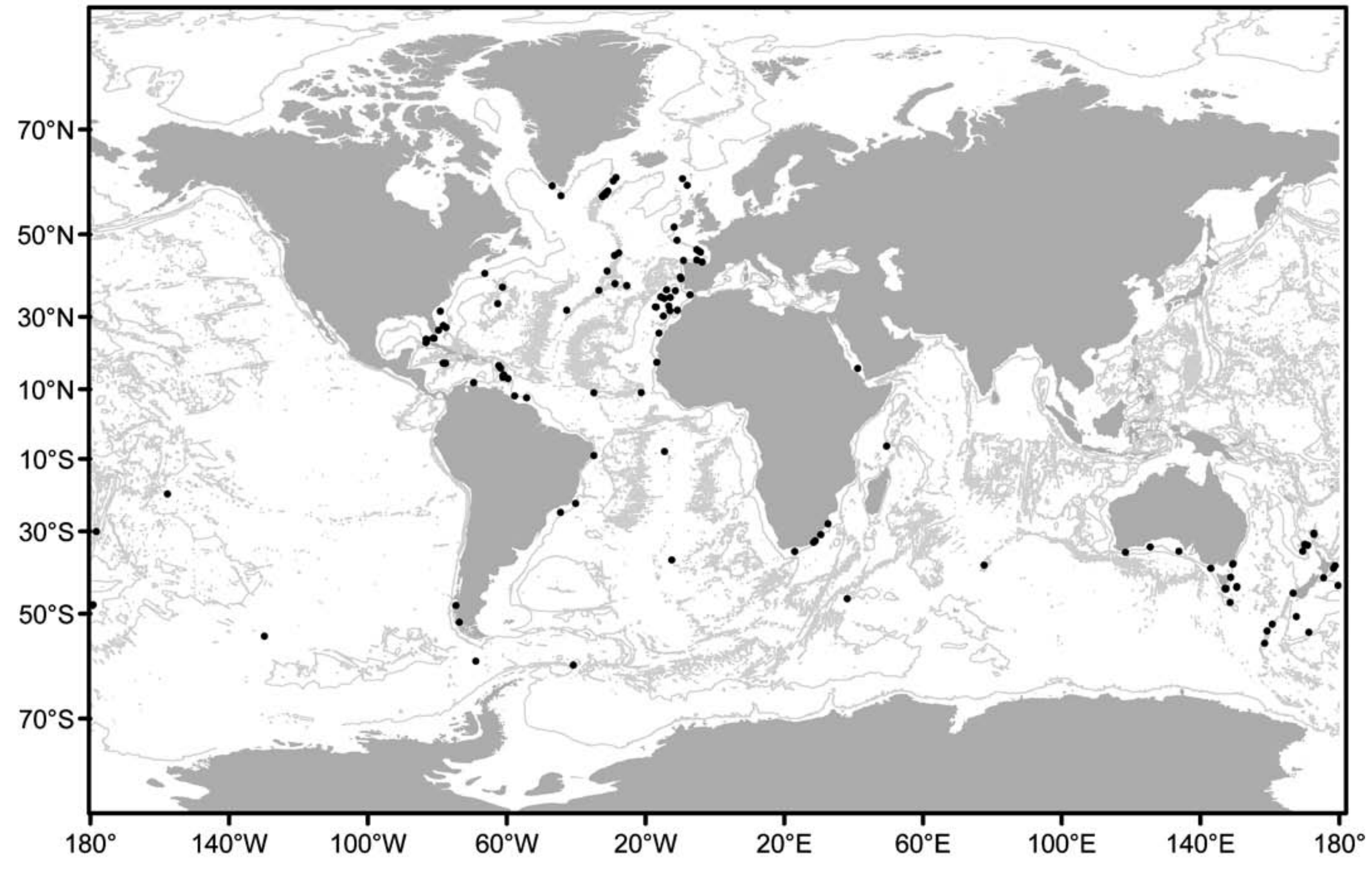

Fig. 2.11 Global distribution of *Solenosmilia variabilis* (isobaths at 2000 m, 5000 m and 9000 m depth).

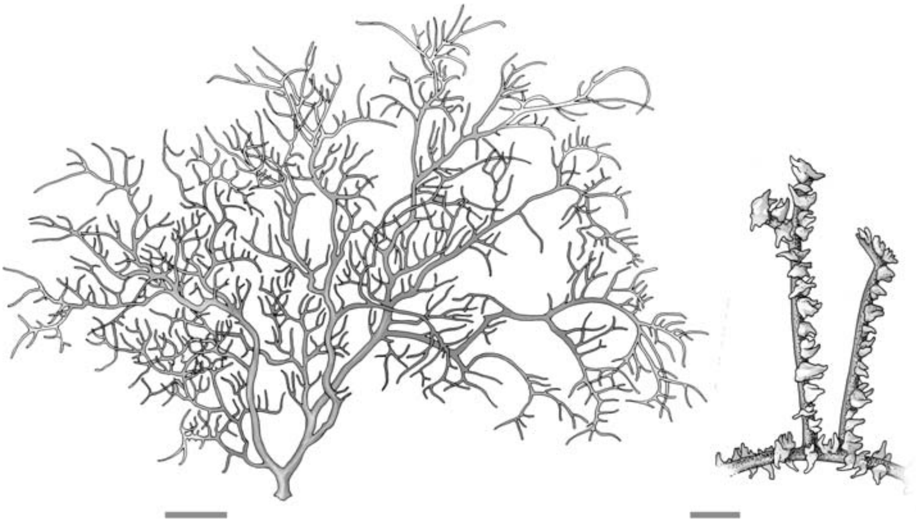

Fig. 2.12 Drawing of a colony of the antipatharian coral *Leiopathes* showing the complex structure it forms with details of individual polyps from a preserved specimen. Scale bars: 50 mm (coral colony) and 3 mm (polyp detail).

perpendicular to the current, and usually occurring on ridges and walls where the current is strong (Parrish, 2007; Parrish & Baco, 2007). Being large, sturdy and exposed to brisk currents, colonies of *Gerardia* are ideal substrata for other associated invertebrates, including other zoanthids, ophiuroids, galatheid crabs, hydroids and sponges, to name but a few.

2.2.3 Antipatharia

A majority of black coral species occur in deep water (Table 2.1), some as deep as 8600 m, and, like most of the other benthic cnidarian groups discussed in this chapter, they are widely distributed throughout the world's oceans from off Antarctica to within the Arctic Circle off Greenland. Their skeletons are composed of chitin complexed with proteins (Goldberg *et al*., 1994). Many species are used as jewellery and statuary (Grigg, 2002), especially those found in the Hawaiian archipelago, off Japan and the Mediterranean. Because they have hard, but flexible, internal axes, they have been used in isotopic studies of growth rate and aging (see Sections 3.4.1, p. 88 and 3.4.2, p. 91) and like the gold coral *Gerardia*, individual cold-water antipatharians may be very long-lived with some, such as *Leiopathes* (Fig. 2.12), living for over 2000 years (see Section 3.4.2, p. 92). No comprehensive list of antipatharian species has been published, but Opresko (2006) is methodically revising the six families in this order, each of his works including keys to the various genera and sometimes the included species.

Table 2.4 *Potential habitat-forming cold-water Antipatharia (compiled with the advice of D. Opresko).*

- Family Antipathidae
    - *Antipathes atlantica* Gray, 1857
    - *A. caribbeana* Opresko, 1996
    - *A. curvata* van Pesch, 1914
    - *A.* sp. cf. *curvata* van Pesch, 1914 (= *A. 'dichotoma'* from Hawaii)
    - *A. dendrochristos* Opresko, 2005
    - *A. grandis* Verrill, 1928
- Family Aphanipathidae
    - *Aphanipathes* (4 species)
- Family Cladopathidae
    - *Chrysopathes* (2 species)
    - *Sibopathes* (2 species)
    - *Trissopathes* (3 species)
- Family Stylopathidae
    - *Stylopathes americana* (Duchassaing & Michelotti, 1860)
    - *Tylopathes* (2 species)
- Family Myriopathidae
    - *Plumapathes pennacea* (Pallas, 1776)
    - *Tanacetopathes hirta* (Gray, 1857)
- Family Schizopathidae
    - *Bathypathes alternata* Brook, 1889
    - *Dendropathypathes boutillieri* Opresko, 2005
    - *Lillipathes* (2 species)
    - *Parantipathes tetrasticha* (Pourtalès, 1868)
    - *Stauropathes* (2 species)
- Family Leiopathidae
    - *Leiopathes acanthphora* Opresko, 1996
    - *L. glaberrima* (Esper, 1788)

Antipatharia, both unbranched whips and bushy colonies, may attain a height of 3 m, and some species provide niches for other invertebrates and fish. Table 2.4 lists the potential habitat-forming species, this list is based on actual observation of associated organisms and/or by inference based on their large size and local abundance. An excellent example of this phenomenon is *Antipathes dendrochristos*, a large, bushy antipatharian coral recently described from the southern California Bight at 100–406 m. Church and Buffington (1969) earlier described these colonies as 'a small, overcrowded city on a lonesome desert' and ranked this species 'as the most spectacular example of symbiosis that I have encountered in the deep sea'. This observation applies also to dead *A. dendrochristos* skeletons that provide habitat for many other invertebrates (see Chapter 5, p. 142).

2.2.4 Octocorallia

As with the Scleractinia, the approximately 2325 species of deep-water (>50 m) octocorals are ubiquitous in marine waters, occurring from the Arctic to Antarctic and to a depth of 6620 m. Some species, such as the precious corals (family Coralliidae), have been used as jewellery for millennia (Grigg, 1993). And, as in the case of Scleractinia, those species having hard internal skeletons can provide valuable palaeoceanographic archives (see Chapter 7).

A well illustrated and readable introduction to the subclass was published by Bayer (1973). All gorgonian species are keyed in the classic account of Kükenthal (1924), whereas a key to all octocoral genera excluding the pennatulids was published by Bayer (1981) and, as a complement, a key to the pennatulid genera was published by Williams (1995). Other useful keys include those to the genera of the isidids (Bayer & Stefani, 1987; Alderslade, 1998), the chrysogorgiids (Bayer & Stefani, 1988), the ellisellids (Bayer & Grasshoff, 1995), the primnoids (Bayer & Stefani, 1989) and the species of paragorgiids (Sánchez, 2005). No comprehensive list of species has been published; however, Williams (1999) has listed all pennatulid species and he also supports a web page titled Octocoral Research Center: www.calacademy.org/research/izg/isg_researchl_ink.htm. This includes a key to the octocoral families, a complete bibliography of octocoral literature, and a list of all octocoral genera with estimated numbers of species contained within.

The habitat-forming deep-water octocorals listed in Table 2.5 are less well known than their scleractinian analogues, and thus are listed only to the generic level, with an indication of how many species occur in those genera, although not all those species are presumed to have habitat-forming capacity. These genera are listed based on their large size and probable high local abundance as well as the quality of their axial structure, a solid axial structure having the potential to accumulate over time and contribute to cold-water coral banks. Most octocorals have a certain degree of flexibility conferred to them by a non-rigid internal axis, which allows them to bend with water currents, an ability not found in the Scleractinia or Stylasteridae. The only octocoral exceptions are the precious corals of the family Coralliidae, which have rigid axes. Genera of the various families are discussed below.

Species of the family Paragorgiidae (the ‘bubblegum corals’, Fig. 2.13) are among the largest and most important sessile benthic invertebrates in the ocean (Sánchez, 2005), having a cosmopolitan distribution and occurring as deep as 4152 m (see Colour plates 10, 21, 23). Colonies up to 10 m in height have been reported off New Zealand by Smith (2001), see Fig. 2.14, justifying its specific name of *Paragorgia arborea*, as large as a tree. Although its axis is not well consolidated, the sheer size of these corals provides ample habitat for numerous fish and invertebrates (Krieger,

Table 2.5 *Potential habitat-forming cold-water Octocorallia with the most significant cold-water taxa shown in bold face.*

- Subclass Octocorallia
  - Order Gorgonacea
    - Suborder Scleraxonia
      - Family Paragorgiidae
        - ***Paragorgia* (14 species)**
      - Family Coralliidae
        - ***Corallium* (19 species)**
        - *Paracorallium* (7 species)
    - Suborder Holaxonia
      - Family Plexauridae
        - *Alaskagorgia aluetiana* Sánchez & Cairns, 2004
        - *Paramuricea grandis* Verrill, 1883
    - Suborder Calcaxonia
      - Family Chrysogorgiidae
        - *Metallogorgia* (2 species)
        - *Iridogorgia* (3 species)
      - Family Primnoidae
        - ***Primnoa* (5 species)**
        - *Callogorgia* (27 species)
        - *Calyptrophora* (13 species)
        - *Narella* (33 species)
        - *Paracalyptrophora* (6 species)
        - *Plumarella* (20 species)
        - *Thouarella* (34 species)
      - Family Isididae
        - *Acanella* (11 species)
        - ***Isidella* (4 species)**
        - *Keratoisis* (25 species)

1993; Koslow *et al.*, 2001; Krieger & Wing, 2002) with Buhl-Mortensen and Mortensen (2004a, 2005) reporting 47 invertebrate species and 1264 individuals from 13 samples of live and dead *P. arborea* from Atlantic Canada.

The 'precious corals' (*Corallium* and *Paracorallium*) are unique among the structure-forming species in having a rigid, non-flexible axis composed of fused sclerites. They occur from New Zealand (F. M. Bayer, personal communication, 2007) to the Gulf of Alaska (Heifetz *et al.*, 2002), as well as the Mediterranean and the western Atlantic, to depths of 3150 m (F. M. Bayer, personal communication, 2007). Their colonies, which rarely exceed 1 m in height, are usually flabellate, the plane of the fan oriented perpendicular to the current. Several of these species, along with the zoanthid *Gerardia* and the scleractinian *Enallopsammia rostrata*, produce complex habitats at 400–600 m along the Hawaiian

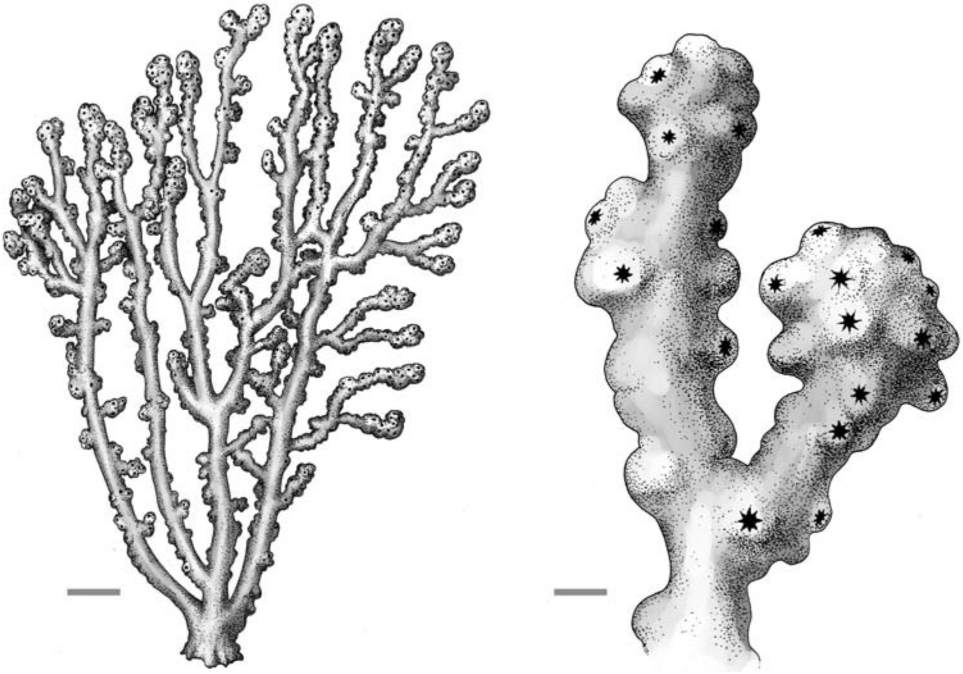

Fig. 2.13 Drawing of a colony of the gorgonian coral *Paragorgia arborea* showing its branching structure and details of individual polyps from a preserved specimen. Scale bars: 50 mm (coral colony) and 10 mm (polyp detail).

Island archipelago, each colony harbouring dozens of associated invertebrates, especially Crustacea.

The plexaurids *Alaskagorgia aleutiana* (Aleutian Islands, 125–512 m) and *Paramuricea grandis* (Georges Bank and New England Seamounts, to 1150 m) are included because of their size and abundance but they are unlikely to provide long-lasting habitat. Being holaxonians, their axes are composed of flexible gorgonin surrounding a hollow, cross-chambered core, thus, although highly flexible, once dead their skeletons do not persist very long on the seafloor.

The remaining families are all calcaxonians, meaning that their flexible axes are solid, composed of gorgonin impregnated with large amounts of calcium carbonate. The genera listed are those that are large and that often occur in significant numbers locally, often providing habitat for other animals. *Metallogorgia* and *Iridogorgia* (family Chrysogorgiidae: the 'golden corals') occur as tall (up to 3 m) dichotomously branched or elegantly spirally branched colonies respectively. Both genera are common in the Hawaiian archipelago and the New England Seamounts (Watling & Auster, 2005) at depths of 900–2100 m, and are generally cosmopolitan in deep water. Seven genera of primnoids are included on

Fig. 2.14 *Paragorgia* can reach huge sizes with individual colonies up to 10 m in height. This example shows the large base of such a colony (probably *P. arborea*) recovered from fishery bycatch off New Zealand (Smith, 2001), another example is given in Colour plate 10. Photograph courtesy of A. Blacklock.

the list as potential structure formers, the most significant being *Primnoa resedaeformis* (Fig. 2.15), known from the North Atlantic at depths of 91–1020 m (Cairns & Bayer, 2005). Records from the Smithsonian Institution's collections show that New England fishers of the nineteenth century frequently brought up this species while fishing on Grand and Georges Banks. Other *Primnoa* species occur in the North Pacific and sub-Antarctic South Pacific (Cairns & Bayer, 2005) to depths of 915 m. Krieger and Wing (2002) report *Primnoa* in the Gulf of Alaska as large as 2 m in height and 7 m wide; they also list some of the predators and symbionts found with this species. *Primnoa notialis* (Cairns & Bayer, 2005) is known to occur only on sub-Antarctic seamounts on the Heezen Fracture Zone of the Eltanin Fracture Zone System at depths of 549–915 m, the site of prodigious cold-water coral banks composed primarily of the scleractinian *Solenosmilia variabilis* (see Cairns, 1982). Etnoyer and Morgan (2005) mapped the distribution of *Primnoa* in the northeast Pacific in the context of habitat-forming taxa, and Buhl-Mortensen and Mortensen (2004a, 2005) discussed the many associated invertebrates of *Primnoa* from Canadian waters.

The bamboo corals (family Isididae) are unique in having a slightly flexible, jointed axis consisting of elongate, inflexible internodes composed of calcium

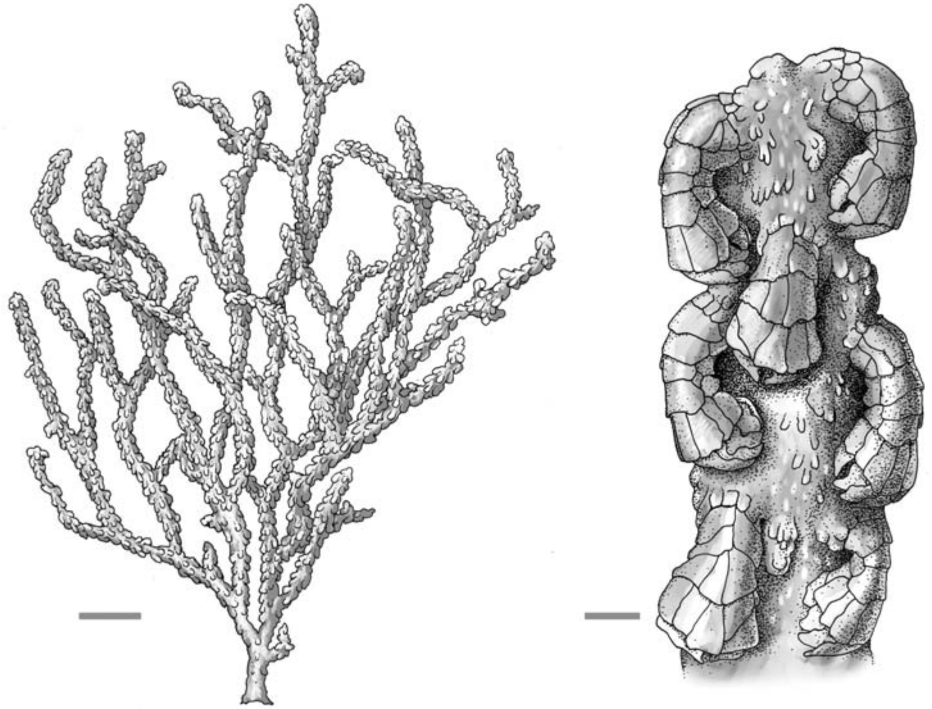

Fig. 2.15 Drawing of a colony of the gorgonian coral *Primnoa resedaeformis* showing its branching structure and details of individual polyps from a preserved specimen. Scale bars: 30 mm (coral colony) and 1 mm (polyp detail).

carbonate. These are joined by short flexible nodes consisting of a black ‘gorgonin’ scleroprotein and together resemble a bamboo stalk in form. Isidids can be large (1–2 m high) and bushy, flabellate or flagelliform (up to 3 m long; Morgan *et al*., 2006). Isidids are cosmopolitan in distribution and occur to depths of 4850 m (Bayer & Stefani, 1987), the three listed genera being common in the North Atlantic, Japan, Indonesia, the Hawaiian Islands and New Zealand. As with the zoanthid *Gerardia*, some isidids bioluminesce when disturbed (Muzik, 1978).

2.2.5 *Stylasteridae*

Stylasterids are ubiquitous in the marine realm, occurring from off Antarctica to the Bering Sea and north of Iceland, the deepest specimen collected at 2789 m (Cairns, 1992a). An example, *Stylaster erubescens*, is illustrated in Fig. 2.16. Most species occur in deep water (Tables 2.1 and 2.6), in fact only one of the 42 species known from the western Atlantic occurs in shallow water (Cairns, 1986). Cairns (1992b) plotted the distribution of all known stylasterids, showing that

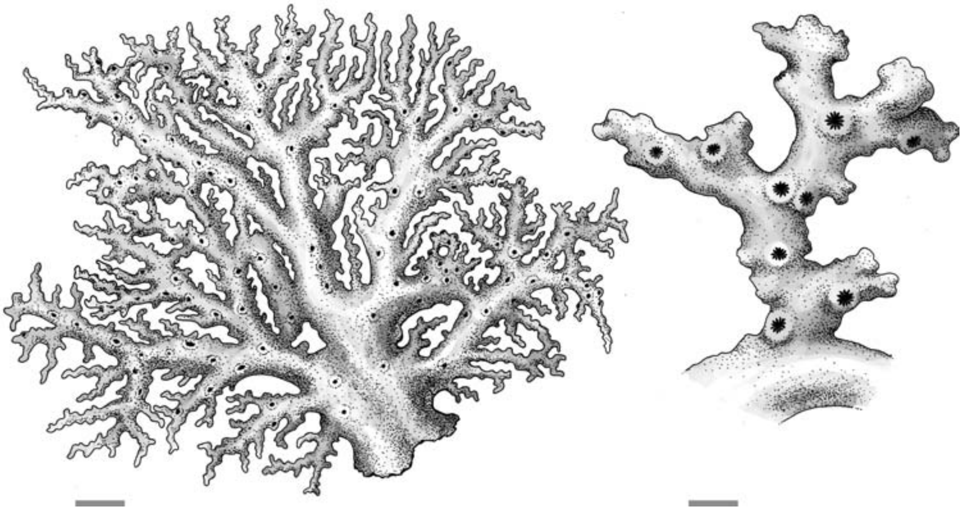

Fig. 2.16 Drawing of a colony of the stylasterid coral *Stylaster erubescens* showing its delicately-branching structure and the details of individual polyp calices. Scale bars: 10 mm (coral colony) and 3 mm (polyp detail).

they have a decidedly insular distribution, being found primarily off small volcanic oceanic islands, atolls, archipelagoes and on seamounts. They are particularly abundant on the Norfolk Ridge, around New Zealand and New Caledonia, the Aleutian Islands, southern South America, Galápagos and the Lesser Antilles, but absent from off continental land masses, such as the Gulf of Mexico (Cairns, 1992b). Surprisingly they are rare to absent off the Hawaiian Islands and off Bermuda. Like Scleractinia, the stylasterid skeleton is composed of calcium carbonate and forms a rigid structure. Although most of the stylasterids produce aragonitic skeletons, as do all Scleractinia, a small percentage of species secrete skeletons of calcite (Cairns & Macintyre, 1992). Their carbonate skeletons are often pigmented orange, red, brown, yellow and even violet, and often have as dense a consistency and lustre as that of *Corallium*, and at least one species, *Allopora californica*, has been collected commercially (Gibson, 1981).

The stylasterid genera were revised in 1983 by Cairns, who also listed all species known at that time; a more recent list was published in 1999 (Cairns *et al*., 1999). A key to the genera was published by Cairns (1992a), and Wing and Barnard (2004) have published an illustrated key to the Alaskan species.

Although stylasterids may not be the key species forming deep-water reef frameworks, they certainly contribute to deep-water structure due to the large sizes of their calcium carbonate skeleton, which can be up to 1 m tall. They occur at densities of 10–96 colonies per square metre (Messing *et al*., 1990; Reed *et al*., 2005, respectively) off Florida and also in high concentrations in the Aleutian

Table 2.6 *Potential habitat-forming deep-water Stylasteridae and their distribution.*

Species	Distribution
Calyptrophora reticulata Boschma, 1968	south of New Zealand, 349–2010 m
Distichopora sulcata Pourtalès, 1867	off Cuba, 60–708 m
Errina antarctica (Gray, 1872)	southern S. America, 18–771 m
Errinopora nanneca Fisher, 1938	Aleutian Islands, 95 m
Errinopsis reticulum Broch, 1951	southern S. America, 280–340 m
Stenohelia concinna Boschma, 1964	Galápagos, 166–806 m
Stylaster brochi (Fisher, 1938)	Bering Sea, 95 m
S. californicus (Verrill, 1866)	off California, 50–200 m
S. campylecus (Fisher, 1938)	Aleutian Islands, 517 m
S. cancellatus Fisher, 1938	Aleutian Islands, 517 m
S. densicaulis Moseley, 1879	southern S. America, 357–1244 m
S. eguchii (Boschma, 1966)	circum-Antarctic, 124–830 m
S. erubescens Pourtalès, 1868	North Atlantic, 146–1400 m
S. filogranus Pourtalès, 1871	Straits of Florida, 183–274 m
S. miniatus (Pourtalès, 1868)	South Carolina to Florida, 146–530 m

Islands, as documented by Heifetz (2002) and Stone (2006). Stone referred to these accumulations as 'coral gardens' and reported concentrations of 1.5 stylasterid and 3.9 octocoral colonies per square metre (see Case study 5.2, p. 150). Several stylasterids form structural habitat (Table 2.6) for associated and symbiotic invertebrates and fish, including ophiuroids, the obligate gastropod *Pedicularia* (see Section 5.4.1, p. 161), polynoid polychaetes, copepods, aplacophoran molluscs, brachiopods, bryozoans, sponges and pycnogonids (Zibrowius & Cairns, 1992; Stone, 2006). Table 2.6 is not considered to be a comprehensive list of habitat-forming species, but rather an attempt to list the major species. One of the most remarkable examples of a habitat-forming stylasterid is *Errinopsis reticulum*, a species endemic to southern South America. As its name implies, it is composed of orange sheets of reticulate, anastomosing branches (Fig. 2.17) that produce a fine mesh of hundreds of 1–2 mm diameter openings. Sheets of branches also form at right angles to the main sheet, resulting in rectangular compartments, each of which houses a variety of encrusting and sessile invertebrates. The Alaskan *Stylaster cancellatus* has a somewhat similar morphology.

2.3 Environmental controls on cold-water coral distribution

As mentioned above, ecological categorisations of coral are filled with exceptions. For example, specimens of the 'deep-water' scleractinian genera *Lophelia*

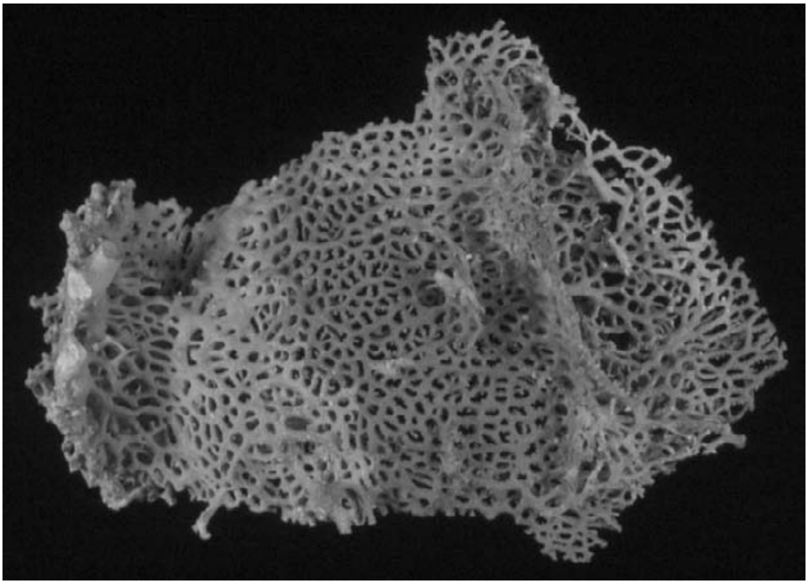

Fig. 2.17 Photograph of *Errinopsis reticulum*. Length of colony is 24 cm.

and *Desmophyllum* and the octocoral genus *Primnoa* can be found in quite shallow water (39 m, 8 m and 2 m, respectively) when environmental conditions are favourable, namely cold upwelled waters associated with fjords. Thus, it is not water depth (hydrostatic pressure) that primarily controls coral distribution but the temperature of the water that seems particularly significant. Each coral species probably has an optimal temperature, and it colonises bathymetrically in response to that range. Examples of equatorial submergence have rarely been documented but do occur, for example *Balanophyllia elegans* (Gerrodette, 1979) and *Leptopenus* (Cairns, 1982), and the location of cold-water coral banks also shows that latitudinal trend. Nonetheless, depth of capture is much more available than temperature of capture, and thus depth is often used as a proxy for purported temperature ranges. Vaughan and Wells (1943) and Chevalier and Beauvais (1987) presented lists of depth ranges for all scleractinian genera. The taxonomy has changed significantly since those lists and many more specimens have been collected, so we present a revised list of generic depth ranges in Table 2.7.

Whereas temperature may be one of the more important ecological factors influencing distribution, corals must have the appropriate substratum on which to settle and build their skeletons, usually by secreting a substantial basal holdfast. In the case of all cold-water structure-forming species, this would equate to a hard substrate, either calcareous or volcanic, that is large and stable enough to support a large colony subjected to strong currents. Stone and Shotwell (2007) also report that large octocorals may sometimes attach to the skeletons of hexactinellid sponges. Smaller non-structure forming cold-water corals often live unattached on soft substrata or even interstitially in sand, but even the larvae of these species must initially attach to a hard substratum, even if as small as a grain of sand.

A constant or periodic flow of water must be present to bring food and oxygen to sessile corals and to remove sediment and wastes. Thus cold-water corals often concentrate on ridges or rocky outcrops where currents are accelerated, or partition themselves in zones along a lithoherm depending on their current preferences (Messing *et al*., 1990), see Section 3.3.2, p. 77. Cold-water coral colonies are often flabellate in shape, with their fans oriented perpendicular to the water flow and their polyps on the downstream side of the fan, in order to take maximal advantage of the eddies produced by the water flowing through their sieve-like fans. Salinity and dissolved oxygen are fairly constant in deep water and thus are probably not a significant factor influencing distribution at local scales, although recent habitat suitability modelling suggests oxygen levels may play a role in determining distributions over large geographic and/or depth scales (see Section 5.6, p. 172).

When the proper temperature, substratum and current velocity are present, it is likely that deep-water benthic cnidarians will colonise and that some will be large enough to produce habitat-forming colonies. Particularly good settings for this to occur are on the summits and flanks of seamounts (e.g. Norfolk Ridge, New England Seamounts, northwest Hawaiian Islands Seamounts and sub-Antarctic Eltanin Fracture Zone; Rogers *et al*., 2007; also see Section 5.3, p. 158), steep-sloped islands (e.g. Hawaiian Islands, western Aleutian Islands, Lesser Antilles, Banda Sea and New Zealand) and continental slopes (e.g. Straits of Florida). However, as a counter-example to these generalisations, Cairns (1992b) noted that stylasterids rarely occurred off continental land masses, even when conditions were otherwise favourable. He allowed that this distribution might be explained as avoidance of fluctuating salinity or high concentrations of suspended sediment in the water, but concluded that stylasterids, being ecological k-strategists, were being outcompeted by more competitive r-strategists in these nutrient-rich areas. As datasets on cold-water coral distribution become more readily available initial efforts have been made to relate distribution to these key oceanographic factors. For example, Bryan and Metaxas (2006) related the occurrence of two cold-water gorgonian families (Paragorgiidae and Primnoidae) with depth, slope, temperature, current, chlorophyll *a* concentration and substratum. The absence of certain aragonitic scleractinian corals from some geographic regions may also be tied to the depth of the aragonite saturation horizon, as discussed below. Improved understanding of the factors controlling cold-water coral distribution is now allowing models of habitat suitability to be generated and this approach is discussed in some detail in Section 5.6, p. 168.

Table 2.7 *Recent azooxanthellate Scleractinia (14 families, 120 genera, 711 species).*

Taxa	Depth range (m)	Number of deep-water species (total number species)
Suborder Astrocoeniina		
Family Pocilloporidae (1 genus, 8 spp.)		
Madracis Milne Edwards & Haime, 1849	0–1220	7 (8)
Suborder Fungiina		
Family Fungiacyathidae (1 genus, 20 spp.)		
Fungiacyathus (Fungiacyathus) Sars, 1872	69–2200	6
F. (Bathyactis) (Moseley, 1881)	84–6328	14
Family Micrabaciidae (4 genera, 13 spp.)		
Leptopenus Moseley, 1881	221–5000	4
Letepsammia Yabe & Eguchi, 1932	50–710	4
Stephanophyllia Michelin, 1841	15–700	3
Rhombopsammia Owens, 1986	390–1401	2
Family Rhizangiidae (4 genera, 32 spp.)		
Culicia Dana, 1846	0–378	4 (13)
Astrangia Milne Edwards & Haime, 1848	0–263	3 (15)
Oulangia Milne Edwards & Haime, 1848	0–135	2 (3)
Cladangia Milne Edwards & Haime, 1851	20	0 (1)
Family Oculinidae (6 genera, 14 spp.)		
Oculina Lamarck, 1816	0–1050	4 (5)
Petrophyllia Conrad, 1855	0–7	0 (1)
Sclerhelia Milne Edwards & Haime, 1850	18–165	1
Bathelia Moseley, 1881	500–1250	1
Cyathelia Milne Edwards & Haime, 1849	13–366	1
Madrepora Linnaeus, 1758	53–1950	5
Family Anthemiphylliidae (1 genus, 7 spp.)		
Anthemiphyllia Pourtalès, 1878	50–1050	7
Suborder Caryophylliina		
Family Caryophylliidae (43 genera, 294 spp.)		

Table 2.7 (*cont.*)

Taxa	Depth range (m)	Number of deep-water species (total number species)
Caryophyllia (Caryophyllia) Lamarck, 1801	0–2670	58
C. (Acanthocyathus) Milne Edwards & Haime, 1848	37–750	9
Premocyathus Yabe & Eguchi, 1942	22–2360	2
Coenocyathus Milne Edwards & Haime, 1848	2–500	6 (8)
Bathycyathus Milne Edwards & Haime, 1848	26–420	1
Crispatotrochus Tenison-Woods, 1878	77–2505	12
Labyrinthocyathus Cairns, 1979	20–1000	5
Monohedotrochus Kitahara & Cairns, 2005	150–1200	3
Concentrotheca Cairns, 1979	183–772	2
Ceratotrochus Milne Edwards & Haime, 1848	7–678	3
Nomlandia Durham & Barnard, 1952	82	1
Trochocyathus (Trochocyathus) Milne Edwards & Haime, 1848	20–1650	26 (27)
T. (Aplocyathus) Orbigny, 1849	240–760	3
Tethocyathus Kühn, 1923	15–1200	7
Paracyathus Milne Edwards & Haime, 1848	0–1260	21 (23)
Polycyathus Duncan, 1876	0–441	7 (18)
Cladocora Milne Edwards & Haime, 1849	28–480	2
Bourneotrochus Wells, 1984	210–566	1
Stephanocyathus (S.) Seguenza, 1864	220–2553	8
S. (Odontocyathus) Moseley, 1881	543–2200	4
S. (Acinocyathus) Wells, 1984	120–1188	2
Vaughanella Gravier, 1915	500–3018	4
Ericiocyathus Cairns & Zibrowius, 1997	814–1401	1
Deltocyathus Milne Edwards & Haime, 1848	44–5080	25
Heterocyathus Milne Edwards & Haime, 1848	0–319	3 (5)
Conotrochus Seguenza, 1864	80–1078	3

Table 2.7 (*cont.*)

Taxa	Depth range (m)	Number of deep-water species (total number species)
Lochmaeotrochus Alcock, 1902	210–1175	2
Paraconotrochus Cairns & Parker, 1992	59–728	3
Aulocyathus Marenzeller, 1904	84–1716	4
Desmophyllum Ehrenberg, 1834	8–2460	2 (3)
Thalamophyllia Duchassaing, 1870	4–914	4
Dactylotrochus Wells, 1954	73–400	1
Hoplangia Gosse, 1860	0–150	1
Oxysmilia Duchassaing, 1870	46–640	2
Phyllangia Milne Edwards & Haime, 1848	0–112	5 (8)
Colangia Pourtalès, 1871	1–347	1 (4)
Rhizosmilia Cairns, 1978	1–549	6
Sympodangia Cairns & Zibrowius, 1997	212–616	1
Lophelia Milne Edwards & Haime, 1849	39–2775	1
Coenosmilia Pourtalès, 1874	74–622	2
Anomocora Studer, 1878	30–785	5
Pourtalosmilia Duncan, 1884	25–300	2
Phacelocyathus Cairns, 1979	20–355	1
Solenosmilia Duncan, 1873	220–2165	1
Dasmosmilia Pourtalès, 1880	37–600	3
Goniocorella Yabe & Eguchi, 1932	88–1488	1
Confluphyllia Cairns & Zibrowius, 1997	135–385	1
Family Turbinoliidae (23 genera, 57 spp.)		
Alatotrochus Cairns, 1984	180–751	1
Pleotrochus Cairns, 1997	200–1137	2
Australocyathus Cairns & Parker, 1992	16–148	1
Tropidocyathus Milne Edwards & Haime, 1848	50–536	2
Cyathotrochus Bourne, 1905	123–522	2
Deltocyathoides Yabe & Eguchi, 1932	44–635	2
Notocyathus Tenison–Woods, 1880	34–1110	2
Thrypticotrochus Cairns, 1989	95–925	1
Cryptotrochus Cairns, 1988	320–700	3

Table 2.7 (*cont.*)

Taxa		Depth range (m)	Number of deep-water species (total number species)
	Pseudocyathoceras Cairns, 1991	91–183	1
	Idiotrochus Wells, 1935	82–645	3
	Lissotrochus Cairns, 2004	342–367	1
	Dunocyathus Tenison–Woods, 1878	64–549	2
	Holcotrochus Dennant, 1902	9–414	2
	Conocyathus d'Orbigny, 1849	4–367	3
	Turbinolia Lamarck, 1818	9–32	0 (1)
	Sphenotrochus Milne Edwards & Haime, 1848	7–403	13
	Foveolocyathus Cairns, 1997	27–367	4
	Endocyathopora Cairns, 1989	46–100	1
	Trematotrochus Tenison–Woods, 1879	150–576	2
	Kionotrochus Dennant, 1906	44–622	1
	Platytrochus Milne Edwards & Haime, 1848	22–201	4
	Peponocyathus Gravier, 1915	30–988	3
Family	Flabellidae 10 genera, 98 spp.		
	Flabellum (Flabellum) Lesson, 1831	36–2260	24
	F. (Ulocyathus) Sars, 1851	101–3186	17
	Truncatoflabellum Cairns, 1989	2–3010	30 (31)
	Blastotrochus Milne Edwards & Haime, 1848	11–18	0 (1)
	Placotrochides Alcock, 1902	119–1628	4
	Javania Duncan, 1876	30–2165	10
	Placotrochus Milne Edwards & Haime, 1848	6–289	1
	Falcatoflabellum Cairns, 1995	366–402	1
	Monomyces Ehrenberg, 1834	0–410	2
	Rhizotrochus Milne Edwards & Haime, 1848	0–1050	4
	Polymyces Cairns, 1979	69–1203	3
Family	Guyniidae 1 genera, 1 sp.		
	Guynia Duncan, 1872	28–653	1
Family	Schizocyathidae 3 genera, 3 spp.		
	Schizocyathus Pourtalès, 1874	88–1300	1
	Pourtalocyathus Cairns, 1979	349–1006	1
	Temnotrochus Cairns, 1995	321–402	1

Table 2.7 (*cont.*)

Taxa	Depth range (m)	Number of deep-water species (total number species)
Family Stenocyathidae (3 genera, 3 spp.)		
Stenocyathus Pourtalès, 1871	110–1500	1
Truncatoguynia Cairns, 1995	80–334	1
Pedicellocyathus Cairns, 1995	70–194	1
Family Gardineriidae (2 genera, 6 spp.)		
Gardineria Vaughan, 1907	2–1200	5
Stolarskicyathus Cairns, 2004	342–367	1
Suborder Dendrophylliina		
Family Dendrophylliidae (18 genera, 152 spp.)		
Balanophyllia (Balanophyllia) Wood, 1844	0–1150	43 (54)
B. (Eupsammia) Milne Edwards & Haime, 1848	18–124	6
Leptopsammia Milne Edwards & Haime, 1848	3–900	10
Endopsammia Milne Edwards & Haime, 1848	0–73	3
Endopachys Lonsdale, 1845	37–386	2
Notophyllia Dennant, 1899	22–458	3 (4)
Bathypsammia Marenzeller, 1907	183–805	2
Thecopsammia Pourtalès, 1868	183–879	2
Trochopsammia Pourtalès, 1878	532–1472	1
Pourtalopsammia Cairns, 2001	155–775	1
Heteropsammia Milne Edwards & Haime, 1848	1–622	1 (3)
Eguchipsammia Cairns, 1994	25–1050	8
Rhizopsammia Verrill, 1870	0–278	6 (10)
Astroides Quoy & Gaimard, 1827	0–30	0 (1)
Cladopsammia Lacaze-Duthiers, 1897	0–470	5 (6)
Dendrophyllia Blainville, 1830	1–1200	21 (29)
Enallopsammia Michelotti, 1871	110–2165	3
Tubastraea Lesson, 1829	0–110	1 (6)
Dichopsammia Song, 1994	20–30	0 (1)
Incertae Sedis	–	2 (3)
Total		**622 (711)**

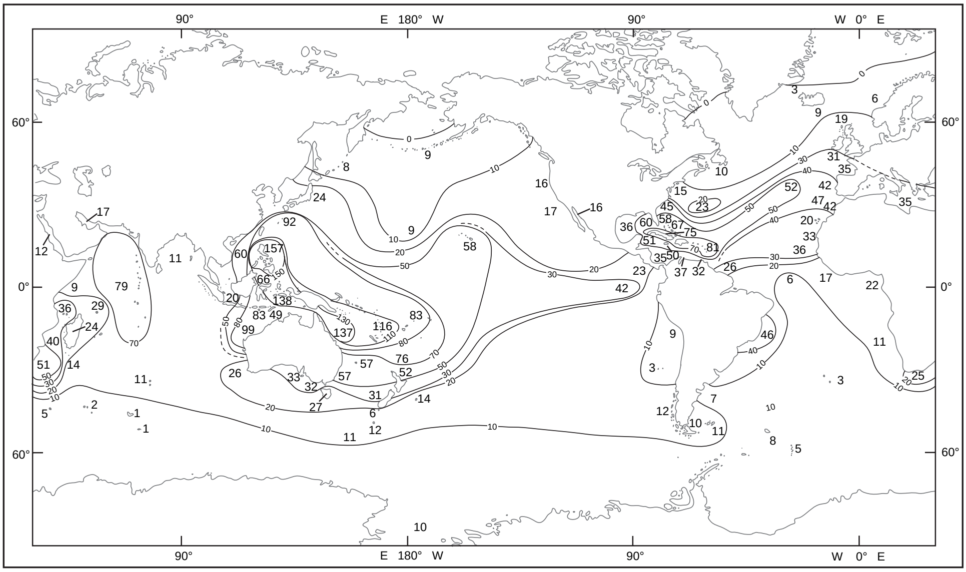

Fig. 2.18 Global species diversity of the 711 azooxanthellate Scleractinia showing three high diversity centres: (1) the region bordered by the Philippines to the north, by New Caledonia to the southeast, including New Guinea and the northeast coast of Australia, (2) the region of the Caribbean from Cuba to the Lesser Antilles and (3) the northwest Indian Ocean. Two other isolated diversity centres can be seen in the southwestern Indian Ocean and off Brazil. Figure reproduced from Cairns (2007), with permission of the Rosentiel School of Marine and Atmospheric Science of the University of Miami.

2.4 Global patterns of cold-water scleractinian diversity

Cairns (2007) recently published a worldwide map of azooxanthellate scleractinian species diversity (Fig. 2.18), admittedly based on species lists from 95 unequally sized regions. Although simple/intuitive in methodology and not mathematically rigorous, the map gives a first approximation of regional azooxanthellate coral species diversity and shows certain trends, i.e. species are most common in the northern hemisphere tropics on the western sides of oceans (see also Keller, 1998). The three regions of highest diversity are: (1) the seas bordered by the Philippines, New Caledonia and New Guinea (120–157 species), (2) the Antilles (81 species) and (3) the northwestern Indian Ocean (79 species). Secondary centres also occur off Brazil (64 species) and the southwest Indian Ocean (51 species). These patterns were found to be remarkably similar to those long known for shallow-water zooxanthellate Scleractinia (see Fraser & Currie, 1996; Cairns, 2007), which have been continually refined over the last half century, although the shallow-water maps were based on genera and the deep-water map on species. Many explanations have been proposed to explain the high diversity of shallow-water corals, and it has become a fairly contentious issue. Many of the theories have been summarised by Fraser and Currie (1996), who favour the 'species richness–energy hypothesis', which stresses the effects of temperature (relating to reproductive success, growth rates, speciation rates) and amount of local substrata for growth, as deciding factors. Regardless, it is empirically obvious that the highest concentration of azooxanthellate species occurs on the shelves and slopes of the largest contiguous area of substrata at 200–1000 m depth (the prime depth for azooxanthellate corals), which has provided a large-scale, heterogeneous variety of bottom topography and habitats available for colonisation.

Whereas this 'area effect' might contribute to high biodiversity in regions such as the Philippines, Antilles, Galápagos and Hawaiian Islands, it does not explain why there are so few azooxanthellate Scleractinia (only 13 solitary species) in equally complex and rugose regions such as the Aleutian and Kurile Islands, where other benthic cnidarians, such as stylasterids and octocorals, abound. However, recent evidence by Guinotte *et al.* (2006) suggests that the depth of the aragonite saturation horizon (ASH), below which corals have greater difficulty in extracting calcium carbonate from the water, may be a limiting factor in cold-water scleractinian coral distribution. The depth of the ASH in this northern boreal region is only about 100 m, compared to 2000 m in the North Atlantic, thus it is not surprising that 8 of the 13 species from the boreal North Pacific have bathymetric ranges shallower than 100 m, and of the remaining 5 species, 4 are fungiacyathids and micrabaciids, species that have adapted to live in a low calcium carbonate environment (Owens, 1984). As noted above, stylasterids are common in this region, but 6 of the 7 species analysed by Cairns and Macintyre (1992) from this region were found to have a calcite skeleton, which occurs in only 28% of stylasterids; calcite has a deeper saturation horizon, allowing them to occur in greater abundance in deeper water. The same is true for octocorals, which have calcitic sclerites. Thus, there might be a mineralogical basis for the distribution of benthic cnidarians in the North Pacific. Regardless of the process that causes high diversity, it is clear that there is a robust pattern that mirrors that of shallow-water corals (Cairns, 2007).

2.5 Molecular phylogeny of cold-water corals

Studies of the molecular phylogeny of cold-water corals have only just begun, but have already shed an interesting light on the relationships between the coral taxa investigated so far. Viewed simply, a molecular phylogeny aims to examine the evolutionary relationships between species, or higher taxonomic levels, based upon similarities or differences in their genetic material. When combined with traditional taxonomic indicators such as morphology, evidence from genetic sequence comparisons has been valuable in developing and revising phylogenies across taxa.

Ribosomal DNA has proved particularly useful in phylogenetic studies, and Hillis and Dixon (1991) provide a thorough review of its use in molecular evolution and phylogeny. We summarise key points of this below and refer the reader to Hillis and Dixon for more detail. Ribosomal DNA, which in eukaryotic cells occurs in both mitochondrial and nuclear genes, has been successfully used in phylogenetic studies for several reasons: (1) it codes for fundamental cellular processes common across all taxa, (2) it is highly conserved making it suitable for comparisons between species, (3) regions of rDNA evolve at variable rates so different regions can be chosen depending on the systematic question being addressed and (4) highly conserved regions in rDNA allow universal primers to bind and initiate DNA replication via the polymerase chain reaction (PCR) to produce multiple copies of the genetic material of interest (see Topic box 2.2).

Distinct rRNA molecules are encoded by rRNA genes and when combined with specific proteins these form ribosomes, the cellular organelles responsible for protein synthesis across living organisms, prokaryotes and eukaryotes alike. Ribsomes are composed of two principal rRNA subunits, known as the small and large subunits (ssu and lsu, respectively), which may also be referred to by their sedimentation velocity units (Svedburg, abbreviated to S so the gene sequences that code for them are referred to as 16S, 18S and 28S for example). The gene sequences for these rRNA molecules and the so-called transcribed signal sequences that help process rRNA transcript (Internal Transcribed Spacers ITS-1 and ITS-2) have all been used in phylogenetic analyses and recently have been used to better understand both phylogeny and interconnectivity of cold-water coral populations.

Choosing genetic material for phylogenetic analysis means selecting a nucleotide sequence conserved sufficiently so that sequences between species can be aligned but not so well conserved that the sequences do not vary enough between taxa to generate a phylogenetic signal (Hillis & Dixon, 1991). The small subunit nuclear gene, between 16S and 18S, has evolved very slowly and so is useful for examining phylogenetic questions across very long time periods (Carboniferous to Middle Devonian, 300–400 Ma) with the most success in reconstructing phylogenies from the Cambrian (630 Ma). In contrast, the large subunit nuclear gene, between 23S and 28S, displays more variable rates of evolution across its domains and it has been largely used for less ancient time periods during the Palaeozoic and Mesozoic (542–100 Ma). Divergent domains in the large subunit rRNA gene have allowed it to be used for more recent time periods (into the

Topic box 2.2 **The polymerase chain reaction (PCR)**

The PCR technique was first developed in the 1980s and through refinements over the intervening years has become an essential component of the molecular biologist's toolkit. Most if not all of the phylogenetic and population genetic studies summarised in this book will have used PCR to amplify the genetic material in question. The PCR reaction produces multiple copies of a DNA sequence from, in theory, just one original source molecule. The only requirement is that the DNA sequences either side of the sequence of interest must be known so that complementary PCR 'primers' can bind to them during the reaction. The chain reaction multiplies the number of copies of the DNA sequence exponentially and can increase the number of copies by more than a million-fold providing enough copies of the sequence for it to be further analysed or sequenced. The concept behind PCR is disarmingly simple. The sequence of events first unzips or denatures the DNA double helix by heating the reaction mixture to more than 90°C. Then the primers designed to match the sequences either side of the one to be amplified are allowed to bind, or anneal, as the mixture is cooled to between 40–60°C. Finally the mixture is heated to 72°C, the temperature at which the enzyme DNA polymerase is active. This enzyme, known as *Taq* polymerase because it was originally isolated from the hot spring bacterium *Thermophilus aquaticus*, continues to rebuild the double helix from the primers' starting point. Thus because the two strands of denatured DNA from the original molecule are rebuilt to form two new DNA molecules, each PCR cycle doubles the number of DNA molecules present. When the cycle is complete the whole process begins again and the stages of denaturation, primer annealing and extension are repeated, exponentially increasing the number of copies, usually cycling over 40 times.

Cenozoic, 66 Ma). Mitochondrial rRNA genes generally evolve far faster than the nuclear rRNA genes making them appropriate for Cenozoic comparisons (Hillis & Dixon, 1991). Finally, the spacer regions of rDNA have been used to examine phylogenies between closely related taxa that have diverged within the last 50 million years (Palaeogene and Neogene). Since these two ITS regions are flanked by the highly conserved 5.8S, 18S and 28S genes, primers have been developed within these conserved genes to amplify the more variable ITS regions making them more amenable to amplification using PCR across a variety of taxa. It is also important to note that mitochondrial DNA from corals seems to evolve far more slowly (10–20 times) than that from other animals perhaps because cnidarians may possess mitochondrial DNA mismatch repair systems not found in other animals (van Oppen *et al.*, 1999).

Ribosomal DNA sequences have proven useful in reconstructing evolutionary relationships between scleractinian corals (e.g. Chen *et al.*, 1995; Romano & Cairns, 2000; Veron *et al.*, 1996; Le Goff-Vitry *et al.*, 2004b; Morrison *et al.*, 2008b). Romano and Palumbi (1996) examined 16S mitochondrial rDNA sequences of 34 coral species from 14 families. They found that the species could be separated into either 'robust' or 'complex' clades that differed in terms of 16S mitochondrial rDNA sequence by almost 30% suggesting that these clades probably diverged from one another before coral skeletons evolved 240 million years ago. Intriguingly this finding implies that the scleractinian coral skeleton has evolved more than once, as was suggested might be the case by Oliver (1980) on the basis of morphological and mineralogical evidence that the Scleractinia evolved from anemone-like ancestors (see Section 6.1, p. 178). The two clades Romano and Palumbi identified from mitochondrial rDNA sequences were called robust and complex because their skeletal architectures differed. The robust clade were corals with solid, heavily calcified skeletons that developed mostly in plate-like or massive growth forms whereas the complex clade tended to form less calcified, relatively porous skeletons developing bushy growth forms. The Caryophylliidae family, to which many cold-water corals belong (see Table 2.7), falls mostly within the robust clade and *Acropora*, the most species-rich scleractinian genus (Veron, 1995), is the archetypal member of the complex clade (Romano & Palumbi, 1996). Le Goff-Vitry *et al*. (2004b) reported on this approach to examine the evolutionary history of two cold-water reef framework-forming corals, *Lophelia pertusa* and *Madrepora oculata*. Their analysis of 16S mitochondrial rDNA sequences from these species grouped both firmly within the robust clade and supported existing classification of *L. pertusa* in the Caryophylliidae (Fig. 2.19). However, *M. oculata* did not cluster with other members of the Oculinidae family where it is currently classified (Wells, 1956), but was the sole current member of the clade between the Caryophylliidae and Pocilloporidae.

The molecular phylogenies provided by 16S mitochondrial rDNA sequence comparisons have also implied that both the suborder Caryophylliina and the family Caryophylliidae have several ancestral lineages (are polyphyletic) because species in these two groups, while largely restricted to the robust clade, are found throughout the scleractinian phylogenetic tree. Perhaps this goes some way to explaining the observation that the Caryophylliina could be considered the most successful of the Scleractinia with many genera and members of this suborder adapted to deep, cold environments (Wells, 1956). Romano and Cairns (2000) produced a molecular phylogeny of the Scleractinia using both nuclear (28S) and mitochondrial (16S) rDNA sequences. Including previously published sequences, they examined 88 species in 20 of the 24 families described by Veron (1995). Their analysis showed that the molecular phylogeny based on mitochondrial DNA sequences could not be reconciled with phylogenies based on morphological data. The skeletal morphology of corals is notoriously variable and scleractinian corals are renowned for the plasticity of their growth forms (Veron,

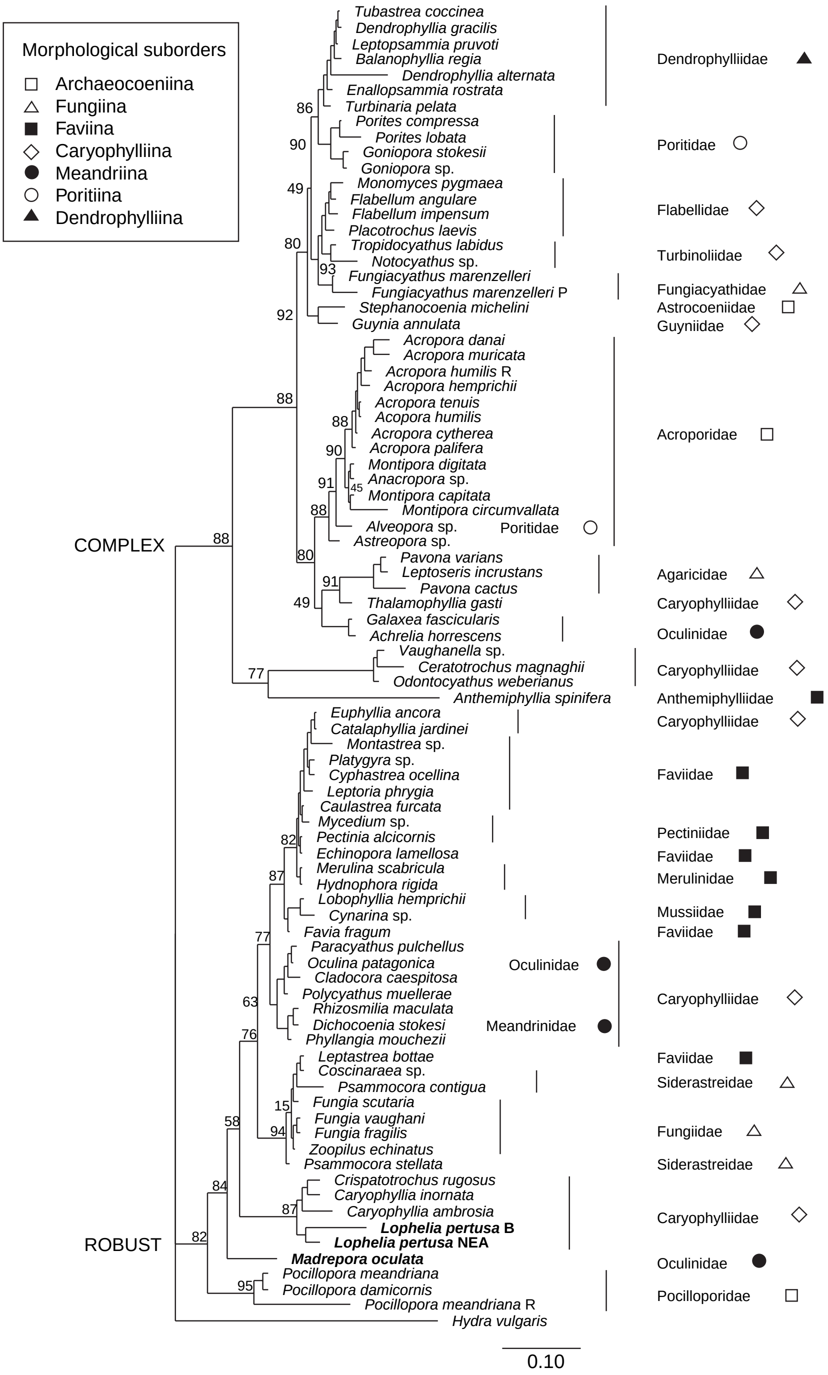

Fig. 2.19 A phylogenetic tree of the Scleractinia, including the cold-water corals *Lophelia pertusa* and *Madrepora oculata* (shown in bold type) examined by Le Goff-Vitry *et al.* (2004b). Probabilities of the partitions, expressed in

1995). Molecular phylogenetic trees derived from mitochondrial rDNA sequences to date imply that the scleractinian coral skeleton may have evolved independently as many as four times from a soft-bodied anemone-like ancestor (Romano & Cairns, 2000). The true sea anemones (Actiniaria) and Corallimorpharia share mesenterial patterns with the Scleractinia (Wells & Hill, 1956) and are commonly regarded as 'scleractinians without skeletons' (Romano & Cairns, 2000; Medina *et al*., 2006). These issues are discussed further in Section 6.1, p. 178.

A final example of the use of mitochondrial rDNA to infer anthozoan phylogeny at higher taxonomic levels comes from work based in part on cold-water corals. France *et al*. (1996) examined mitochondrial 16S rDNA from several cold-water corals sampled from North Pacific seamounts along with a selection of shallow-water anthozoans. By sequencing a variety of species from both the Octocorallia and Hexacorallia, France *et al*. concluded that the Ceriantharia and Antipatharia had diverged from one another, yet grouped with other hexacorals so supporting the two subclasses of the Anthozoa into hexacorals and octocorals, as shown in Table 2.1. Later analysis of the complete mitochondrial genome of the antipatharian *Chrysopathes formosa* also supported the classification of black corals in the subclass Hexacorallia (Brugler & France, 2007).

However, while molecular phylogenies have produced considerable insights into evolutionary relationships within the Scleractinia no overall consensus has as yet been reached regarding relationships among anthozoans. For example in their study of hexacorallian systematics, Daly *et al*. (2003) combined information from molecular and morphological sources and concluded that the Zoanthidae, Antipatharia, Scleractinia and Corallimorpharia formed a 'sister-group', unlike the predominant view that groups the Actiniaria, Corallimorpharia and Scleractinia, and that the scleractinian coral skeleton probably had a single origin. It can be expected that this debate will continue as phylogenetic studies incorporating both molecular and classical approaches are completed on a greater range of anthozoans.

Molecular phylogenetics can also help explain patterns of diversification at lower taxonomic levels. Lindner *et al*. (2008) produced a phylogeny for the stylasterid corals using gene sequences coding for: (1) the large ribosomal subunit of mitochondrial RNA (lsu-rRNA, 16S), (2) the small subunit of nuclear RNA (ssu-rRNA,

Caption for Fig. 2.19 (cont.)
percentages, are shown at node labels. The scale unit is the mean of the posterior probability density. A capital letter by the species indicates the origin of the sample when necessary (*Acropora humilis* R, Réunion Island; *Lophelia pertusa* B, off Brazil; *Lophelia pertusa* NEA, northeast Atlantic; *Fungiacyathus marenzelleri* P, Porcupine Seabight; *Pocillopora meandriana* R, Réunion Island). Figure adapted from Le Goff-Vitry *et al*. (2004b), with permission of Elsevier.

18S) and (3) nuclear calmodulin (CaM). Their analysis included 100 species and showed that stylasterid corals originated and diversified in deep waters (defined as >50 m), supporting previous interpretation of the fossil record (Jablonski, 2005). The molecular data also indicated that the stylasterids evolved protective structures (lids and opercula on feeding polyps) in the deep sea and invaded shallow seas at least three times in evolutionary history.

However, as well as their utility in phylogenetics, molecular approaches can also reveal patterns of linkage and connectivity between populations and we summarise these approaches and their application to cold-water coral species below.

2.6 Linkages and connectivity

Cold-water corals, like many marine organisms, can show remarkable dispersal abilities. Some species even rapidly colonise anthropogenic structures from subsea communications cables to shipwrecks and oil platforms. As discussed more in Section 3.4, p. 83, some of the earliest indications of cold-water coral growth rates came from specimens that had colonised trans-Atlantic telegraph cables in the nineteenth century. But despite this prodigious dispersal potential the larval biology of cold-water corals is not well known and we understand little about how interconnected these habitats are in terms of larval exchange. Critical questions remain to be examined. What proportion of cold-water coral populations arise from asexual reproduction (i.e. are clones)? To what extent are they reliant on self-seeding versus recruitment from other populations? How far can their larvae disperse? What dispersal variability is there between cold-water coral taxa? It is only very recently that any information on the links and connections between cold-water coral habitats has been available.

Conceptually the simplest way to assess larval connectivity between marine populations would be to somehow mark a significant percentage of a larval population, release them and see where they settled, grew and eventually reproduced. In reality marking and recapturing marine larvae in any meaningful numbers, let alone assaying those that survive to reproduce, is extremely challenging. Various approaches, outlined by Thorrold *et al.* (2002), have been developed to mark marine larvae and juveniles including: (1) physical tags (practical only for the largest individuals >5 mm in size), (2) fluorescent markers of calcified tissues (e.g. tetracycline, alizarin and calcein), (3) enriching with specific elements (e.g. strontium to mark juvenile fish scales and otoliths) or radioactive isotopes and (4) inducing thermal marks in otoliths by exposing larval or juvenile fish to temperature fluctuations. Even if such direct tagging methods were developed to the level where significant numbers of marked animals are recaptured, they are most applicable to species with well-known larval biologies that could be recaptured easily in shallow waters. For example, in their study of tropical reef fish recruitment, Jones *et al*. (1999) marked otoliths from approximately 1% of a larval damselfish population (still representing an astounding 10 million marked larvae) and recovered just 15 marked individuals. Given the enormous technical challenges of marking and recapturing marine larvae and the constraints of working at great depths, it seems unlikely that this approach will be helpful in understanding connections between cold-water coral populations.

Therefore, investigations of connectivity of cold-water coral populations have relied on indirect genetic methods that compare genetic markers between populations. But interpreting such studies is difficult because this relies on assessing small genetic differences and then trying to understand how such genetic structuring has come about from a complex interplay of historical and present-day factors. These include long-term changes in plate tectonics, oceanography and climate and on shorter timescales the effects of the demography, ecology and behaviour of the species in question. These factors influence rates and patterns of species dispersal which, along with the survival and reproduction of immigrating individuals, will influence how random genetic drift and natural selection processes shape the genetic structure of a population (Grosberg & Cunningham, 2001). Genetic approaches offer tremendous potential to unravel levels of gene flow between populations but as Grosberg and Cunningham observe 'The literature devoted to inferring levels of gene flow from allelic frequencies is massive, complex, and often arcane.'

Our objective here is to review briefly the means by which population genetic techniques can assess the relationships and levels of connectivity between marine populations and then to consider and summarise how these approaches have been used to study cold-water coral populations. An excellent overall review of population genetics is provided by Hartl and Clark (1997). Understanding population relationships in this way has far-reaching consequences; not just for the immediate and pressing requirements to design marine reserves (see Section 8.2.1, p. 255) but, when considered over evolutionary timescales, to appreciate how populations may have become isolated from one another to set the stage for speciation (see Palumbi, 1994). To assess whether a population is open to genetic exchange with surrounding populations, a suitable marker that varies within the species in question and has a known inheritance is needed (Hellberg *et al*., 2002). The development of allozyme electrophoresis in the 1960s allowed population geneticists to begin characterising the spatial distribution of gene frequencies. Allozymes are genetically distinct versions of enzymes that can be separated and visualised on a support matrix by electrophoresis. Since they are coded by different alleles at a single locus they effectively provide a proxy means of identifying differences at that locus and thereby identifying separate genotypes. Allozyme markers provided the backbone of many population genetic studies until the tools of molecular biology developed to allow an organism's genetic material to be analysed directly, spurred by the 'DNA fingerprinting' revolution of the mid-1980s. Population genetic studies of cold-water corals have only been made relatively recently, since the development of DNA markers from corals.

As well as providing greater resolution in the variation they show, DNA markers have important practical advantages over allozymes. DNA can be easily preserved with chemical fixatives whereas labile enzymes need to be frozen. DNA sequences can be amplified by PCR from tiny initial samples, in some cases even from long-preserved ancient DNA. There is now an impressive array of DNA-derived markers at the molecular ecologist's disposal and these can be thought of in three categories (Herbinger *et al.*, 2003): (1) tandem repeat markers comprising minisatellites (10–100 base pairs) and microsatellites (2–10 base pairs); (2) multilocus markers such as short interspersed nuclear elements (SINEs) and randomly amplified polymorphic DNA (RAPD) and (3) single nucleotide polymorphisms such as restriction fragment length polymorphisms (RFLP). Of these, microsatellites have become the 'marker of choice' for many population genetic studies (e.g. Queller *et al.*, 1993; Selkoe & Toonen, 2006) and have been used by several recent studies of the population genetics of cold-water corals.

The first microsatellite markers from scleractinian corals were described from the shallow-water species *Seriatopora hystrix* (Maier *et al.*, 2001). The following year, Le Goff and Rogers (2002) characterised ten microsatellite loci from the cold-water coral *Lophelia pertusa*. Microsatellites are also known as simple sequence repeats (SSR), variable number tandem repeats (VNTR) and short tandem repeats (STR). These short sequences usually repeat between 5 and 40 times at a locus with dinucleotide, trinucleotide or tetranucleotide repeats being most commonly used in population genetic studies (Selkoe & Toonen, 2006). The DNA either side of a microsatellite locus is conserved so these flanking sequences usually remain unchanged within species, and sometimes between different species. This makes the flanking regions suitable for PCR primers so that the microsatellite sequences can be amplified. Because the microsatellite repeats are subject to frequent DNA replication errors that change the number of repeating units, mutations can rapidly produce alleles of different lengths that can be identified by high-resolution gel or capillary electrophoresis, rather than time-consuming and expensive DNA sequencing. Rapid microsatellite mutation rates of 10^{-2} to 10^{-6} per generation (Schlötterer, 2000) produce levels of allelic diversity high enough to study genetic processes on ecological timescales (Selkoe & Toonen, 2006) and the microsatellites with the highest allelic diversity can provide unique individual markers allowing paternity and clonal structure to be examined (Queller *et al.*, 1993). The latter is particularly relevant to understanding population genetics of cold-water corals because they can reproduce asexually (see Section 3.6, p. 103).

But while there are many advantages to microsatellites there are, naturally, also some disadvantages (reviewed by Selkoe & Toonen, 2006). It takes time to develop the PCR primers to amplify microsatellite sequences and, since microsatellite primer sequences are often quite species-specific, new primers may be needed for each species being studied. Uncertainties in the way microsatellites mutate remain, so care is needed to ensure appropriate mutation models and statistical analyses of allele frequency are used. Microsatellites of different length can be identified cheaply and efficiently by size using gel electrophoresis but this great advantage may become a double-edged sword because alleles of the same length cannot be detected with this approach. This hidden allelic diversity, or homoplasy, takes two forms. In the first, detectable homoplasy, the alleles have different sequences and can be identified by sequencing the microsatellites, but if mutational events reverse themselves (‘back-mutation’) or an allele mutates by chance to the same length and sequence as another this allelic diversity will be impossible to detect. Finally, to be practical and reproducible between research groups, PCR-based amplification must be reliable and a number of workers have reported that amplifying microsatellite DNA from corals and other invertebrates can be problematic (Baums *et al.*, 2005; Shearer *et al.*, 2005; Selkoe & Toonen, 2006).

Using the ten microsatellite loci described by Le Goff and Rogers (2002) and ribosomal ITS sequences, Le Goff-Vitry *et al.* (2004a) examined the genetic structure of *Lophelia pertusa* in the northeast Atlantic from a series of sampling sites between northern Spain and mid-Norway. These studies revealed interesting features of the population genetic structure of this dominant North Atlantic reef framework-forming coral. Their first finding showed that all populations and loci examined deviated strongly from Hardy–Weinberg equilibrium (see Topic box 2.3). Using microsatellites to identify individuals as discrete multi-locus genotypes, Le Goff-Vitry *et al.* were able to examine the proportion of their coral samples that were genetically identical, in other words were clones. They found that the proportion of clones in their sample set varied rather dramatically, with the Darwin Mounds in the northern Rockall Trough (Masson *et al.*, 2003) dominated by clonal individuals. This could be explained by low recruitment from external populations and a local population derived in large part from asexual reproduction (Le Goff-Vitry *et al.*, 2004a). Interestingly, a parallel histological study of the Darwin Mounds’ *L. pertusa* population by Waller and Tyler (2005) found no evidence for reproduction and speculated

Topic box 2.3 **Hardy–Weinberg equilibrium, the Wahlund effect and null alleles**

The Hardy–Weinberg equilibrium is a fundamental population genetic principle, named for the early twentieth-century work of British mathematician Godfrey Hardy and German physician Wilhelm Weinberg. It states that the occurrence of a genotype in a randomly mating population will stay constant unless mutations accumulate or the assumption of random mating is violated. This model explains Mendelian genetic segregation for all sexually reproducing diploid organisms by describing the relationship between allele frequencies and genotype frequencies in a population assuming: (1) populations are randomly mating, (2) there is no mutation, (3) population sizes are large, (4) there is no natural selection and (5) sampling is carried out from an isolated population with no immigration.

The frequency of genotypes and alleles is therefore at equilibrium and deviations from equilibrium can be used to understand factors influencing a population's genetic structure. This can be represented in the simplest sense by considering two alleles, one dominant (A) and one recessive (a) occurring with the frequencies p and q respectively:

		Females	
		A(p)	**a(q)**
Males	**A(p)**	AA(p^2)	Aa(pq)
	a(q)	Aa(pq)	aa(q^2)

Assuming random mating and an infinite population size this gives the following three possible Hardy–Weinberg genotype frequencies (Fig. 2.20):

$$f(\mathrm{AA}) = p^2 \tag{Eq. 2.1}$$

$$f(\mathrm{Aa}) = 2pq \tag{Eq. 2.2}$$

$$f(\mathrm{aa}) = q^2 \tag{Eq. 2.3}$$

and thus

$$p^2 + 2pq + q^2 = 1 \tag{Eq. 2.4}$$

Distortions to the Hardy–Weinberg equilibrium come from a variety of causes. Natural selection may alter the fitness of certain genotypes and migration of individuals with different genotype frequencies will both shift this equilibrium. Assortative mating with similar genotypes produces excess homozygotes or with dissimilar genotypes produces excess heterozygotes. Mating within subpopulations increases the frequency of homozygotes and in extreme cases can lead to inbreeding. Mutations may produce new alleles but in reality this is extremely rare and selection will quickly counter-balance deleterious mutations. Finally, random genetic drift

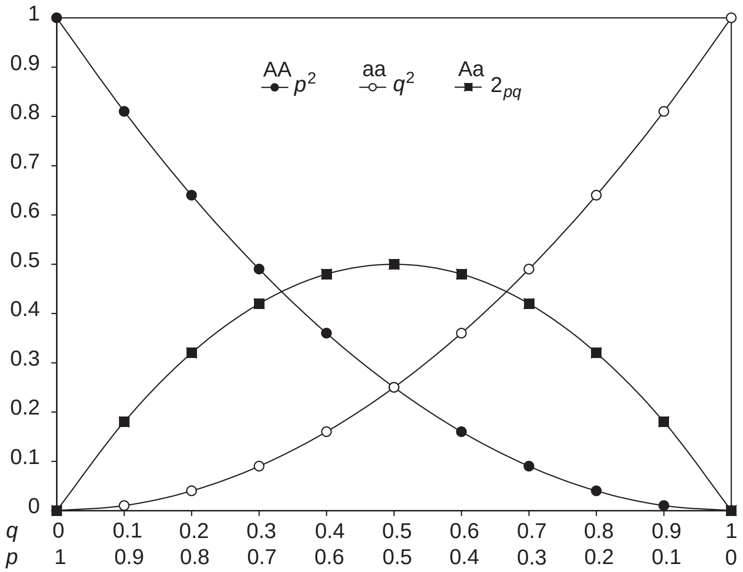

Fig. 2.20 Graphical representation of the Hardy–Weinberg principle where the horizontal axis shows allele frequencies p and q and the vertical axis shows the resulting genotype frequencies.

events can cause small deviations from Hardy–Weinberg equilibrium that may accumulate over long time periods and or become particularly significant in small populations. Studies of population genetics need selectively neutral markers so that factors that influence population structure such as genetic drift, migration or bottlenecks can be examined.

The most common deviation from Hardy–Weinberg equilibrium is a deficit of heterozygotes, typically caused by factors such as strong inbreeding or selection against an allele. However, fewer heterozygotes than predicted may also be found if two genetically distinct groups are sampled and analysed as one. This is known as the Wahlund effect after Swedish genetist Sten Wahlund who first documented this phenomenon in the 1920s. This could happen because the two groups occur together but rarely breed or because the sampling scale is larger than the population scale. These factors could easily affect studies of cold-water coral habitats where the constraints of deep-water sampling may be biased geographically and lack of basic knowledge of the extent of coral populations limits our understanding of their spatial scale. However, these causes of heterozygote deficit should be detectable since they will affect all loci, not just a few (Selkoe & Toonen, 2006).

Another common cause of heterozygote deficit is a failure in the mechanics of the technique used to assay microsatellite diversity. 'Null alleles' are alleles that fail to amplify in a PCR either because the reaction conditions are inappropriate or there have been mutations in the primer-binding regions. Null alleles can be detected by first seeing whether DNA from suspected individuals fails to amplify time after time and then using statistical approaches to examine whether the observed pattern of heterozygote deficit can be explained by the factors outlined above or point to the presence of null alleles. A low incidence of null alleles is not thought to be a major source of error but their effect on estimates of genetic differentiation has not yet been fully investigated (Selkoe & Toonen, 2006).

that this might be related to disturbance by bottom trawl fishing in this area (Wheeler *et al*., 2005b, see Section 8.1.1, p. 237). When they compared gene diversity indices calculated from just the sexually produced corals, Le Goff-Vitry *et al*. found the lowest genetic diversity in *L. pertusa* sampled from an isolated Norwegian fjord, Osterfjord, and evidence that both the fjord and Darwin Mounds' corals might have experienced population bottlenecks. In contrast to the genetic differentiation of the fjord subpopulation, *L. pertusa* populations from the European continental shelf showed only moderate but still significant genetic differentiation suggesting that some level of gene flow is taking place along the continental margin. This is supported by some evidence that *L. pertusa* larvae may be lecithotrophic (Waller & Tyler, 2005, Section 3.6, p. 100) and that coral larvae survive long enough in the plankton to have colonised northern North Sea oil platforms exposed to Atlantic bottom waters (Roberts, 2002; Gass & Roberts, 2006). The evidence for significant levels of asexual reproduction and potential population bottlenecks all help explain the strong deviations from Hardy–Weinberg equilibrium recorded in *L. pertusa* in the northeast Atlantic (Le Goff-Vitry *et al*., 2004a).

Subsequently, Morrison *et al*. (2008b) completed a similar analysis of the *L. pertusa* populations from the Gulf of Mexico and US South Atlantic Bight with a few outlying samples from the northeast Atlantic. Because initial attempts to use the microsatellite markers developed by Le Goff and Rogers (2002) failed, Morrison *et al*. (2008a) developed 13 further microsatellite markers of which 9 were used by Morrison *et al*. (2008b) to assay population structure in the Gulf of Mexico and US South Atlantic Bight. This first comparison of cold-water coral population genetics across ocean basins produced complex results with genetic structuring seen at a variety of scales between adjacent sites and geographic regions. By using a technique to calculate pairwise genetic distances between sites (chord distances), Morrison *et al*. showed that *L. pertusa* populations tended to group by ocean basin, suggesting that at this large scale the populations have evolved distinct genetic differences (Fig. 2.21). On balance, the pattern of genetic variation across the Gulf of Mexico, US South Atlantic Bight and northeast Atlantic indicated a stepping-stone model of population structure with gene flow between geographically close populations but levels of genetic exchange diminishing with distance apart so that the most distant populations were isolated by distance (Morrison *et al*., 2008b).

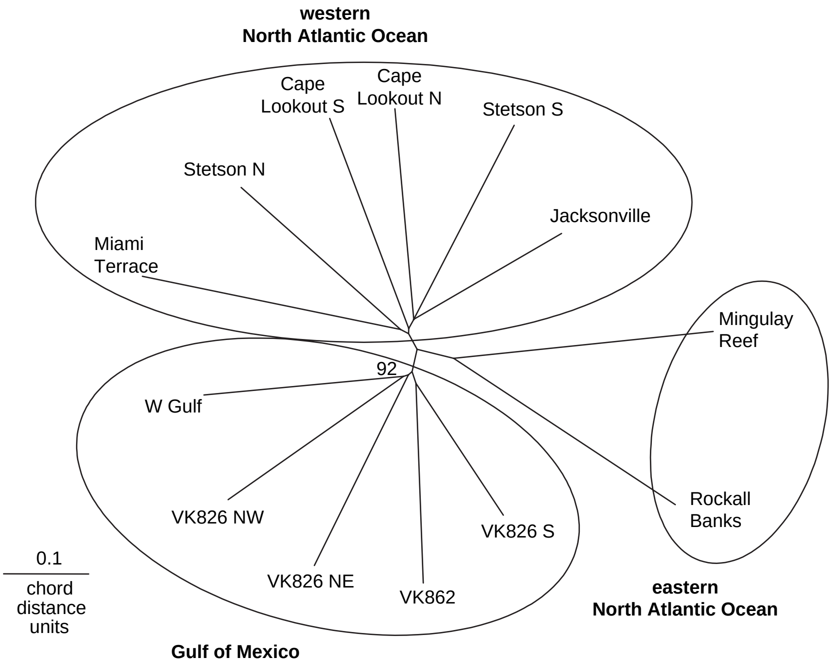

Fig. 2.21 Genetic relationships between *Lophelia pertusa* populations sampled from the Gulf of Mexico, US South Atlantic Bight and northeast Atlantic. Figure shows an unrooted neighbour-joining tree generated from pairwise genetic distances ('chord distance') derived from multilocus microsatellite genotypes. The number at the Gulf of Mexico node represents bootstrap support, see Morrison *et al.* (2008b) for details. Figure reproduced from Morrison *et al.* (2008b), courtesy of the United States Geological Survey.

Precious corals (see Section 2.2.4, p. 37) have also come to the attention of population geneticists because these populations have been heavily harvested to provide material for jewellery and concerns have been raised that without careful management local populations could be driven to extinction. The first allozyme-based study of Mediterranean *Corallium rubrum* showed that relatively shallow (up to 50 m), cave- or cliff-dwelling populations of red coral taken from two locations in the Tyrrhenian Sea off Italy were significantly different from one another (Abbiati *et al.*, 1993). While most loci from one site were in Hardy–Weinberg equilibrium, those from the second site were not and had a significant deficit of heterozygotes. This was explained by the Wahlund effect (see Topic box 2.3) in that the cave-dwelling corals sampled at this site may have formed genetically distinct units both because of the naturally isolating nature of the cave structures and the tendency of red coral larvae to be negatively geotactic and so become trapped within them (Abbiati *et al.*, 1993). It is likely that more information on the levels of gene flow between Mediterranean *C. rubrum* will become available following the recent development of seven microsatellite markers for this species (Costantini & Abbiati, 2006).

Similar conservation concerns have spurred research into the closely related precious coral *Corallium lauuense*, which is collected for jewellery from the Hawaiian Seamounts. Using a manned submersible, Baco and Shank (2005) collected 134 of these precious corals from eight seamount sites between depths of 385–575 m. From this collection they successfully amplified three microsatellite loci that revealed departures from Hardy–Weinberg equilibrium again with significant heterozygote deficiencies. As with the Mediterranean *C. rubrum*, these deficiencies were probably related to the Wahlund effect, since very little is known about the population boundaries of this species. However, Baco and Shank also found evidence of significant levels of inbreeding in these populations that would also contribute to these heterozygote deficiencies. In turn, the high levels of inbreeding may relate to intensive fishing pressure in the 1970s that could have caused a temporary population bottleneck if it reduced recruitment from neighbouring sites. Curiously, although the *C. lauuense* populations in Hawaii were spaced between seamounts in a classic stepping-stone manner, they did not appear to be clearly isolated from one another by distance. Instead some neighbouring populations were more genetically distant from one another than populations that were geographically distant (see Section 5.3, p. 158). As with the Mediterranean *C. rubrum* population, it is likely that more information on the population genetics of *C. lauuense* will become available following the recent characterisation of more microsatellite loci (Baco *et al*., 2006).

Thus it is clear that molecular genetic approaches are beginning to help us understand population relationships between cold-water coral habitats. But to interpret these patterns we need to understand the biology of the individual coral species, in particular their reproductive strategies. The last ten years have seen exciting developments in our basic understanding of cold-water coral biology and we consider these findings in the next chapter.

3

Biology

The great lesson which it reads is, that vital processes can go on in certain animals at prodigious depths, and in much cold, quite as well as in less depths and in considerable heat. It suggests that a great number of the Invertebrata are not much affected by temperature, and that the supply of food is the most important matter in their economy.

On the *Madreporaria* dredged up in the Expedition of *HMS Porcupine*
P. Martin Duncan (1870)

A sound appreciation of the biology of coral habitats must be grounded in understanding both the geological and hydrographic contexts in which these habitats have developed. As sessile, structure-forming species dependent on water flow to supply food, exchange gametes and disperse larvae, corals are intimately related to near-seabed hydrography and, in turn, their occurrence on continental shelves, slopes and seamounts may help interpret flow and turbulence regimes in these dynamic regions of the world's oceans. In this chapter, we consider both the structural and functional biology of the major groups of cold-water corals described in Chapter 2. We outline the major hypotheses that have been advanced to explain coral occurrence and review currently available evidence. Finally, and perhaps most significantly, we note that many aspects of the basic biology of cold-water corals are either unknown or have only been examined very recently. For this reason elements of the chapter will necessarily be brief but will include notes on where we can expect advances as the scientific community capitalises on our improved geological understanding of cold-water coral distribution and occurrence and begins to address fundamental questions on seasonality, food supply, ecophysiology, growth and reproduction. For the biological sciences, these are truly exciting times to work on cold-water corals.

Table 3.1 *Partial classification of the phylum Cnidaria, showing the five major cold-water coral taxa (in bold type).*

- Phylum Cnidaria
- Subphylum Anthozoaria
  - Class Anthozoa
    - Subclass **Octocorallia** (= **Alcyonacea**)
    - Subclass Hexacorallia (= Zoantharia)
      - Order **Scleractinia** (the stony corals)
      - Order **Antipatharia** (the black corals)
      - Order **Zoanthidea**
      - Order Corallimorpharia
- Subphylum Medusozoa
  - Class Scyphozoa (jellyfish)
  - Class Hydrozoa (hydroids)
    - Subclass Hydroidolina
      - Order Anthoathecata
        - Family **Stylasteridae**
      - Order Leptothecatae

3.1 Anatomy

All cold-water corals belong to the phylum Cnidaria. This phylum is biradially symmetrical, with adult corals and sea anemones composed of a central mouth surrounded by a ring of tentacles when viewed from above. All Cnidaria are characterised by stinging cells or cnidocytes (giving the phylum its name from the Greek *knide* or nettle). Nematocyst-laden cnidocytes both defend corals from predators and help them capture and kill prey. Cold-water coral feeding, growth and physiology is described in more detail later in this chapter.

One way to get a feeling for the diversity of corals (as defined in Chapter 2) and how they are related to one another is to see them placed in a formal higher classification. The partial classification in Table 3.1, abstracted from Marques and Collins (2004), is labile and subject to revision as more is learned about the various cnidarian taxa, and, as can be seen from the table, consists of coral groups ranging from the subclass to the familial level.

Another way to conceptualise the differences among coral taxa is through a dichotomous key (Fig. 3.1), which shows that the five coral groups can be distinguished based on characteristics of their mesenteries, tentacles and skeleton. To use this key one should know that a coral polyp can be abstractly visualised as a hollow cylinder that terminates distally in a flat oral disc, the centre of which bears the mouth, which is usually surrounded by a ring or several rings of

1	Gastrovascular cavity not divided by mesenteries; stomadeum absent	**Stylasteridae**
1′	Gastrovascular cavity divided by mesenteries; stomadeum present	2
2	Mesenteries paired	3
2′	Mesenteries unpaired	4
3	Calcareous exoskeleton; mesenteries complete	**Scleractinia**
3′	Skeleton sometimes present as dense proteinaceous layers; some mesenteries incomplete	**Zoanthidea**
4	Tentacles pinnate, 8 in number; also 8 mesenteries	**Octocorallia**
4′	Tentacles simple, 6 in number; 6, 10 or 12 mesenteries	**Antipatharia**

Fig. 3.1. Dichotomous key showing that the five coral groups can be distinguished based on characteristics of their mesenteries, tentacles and skeletons.

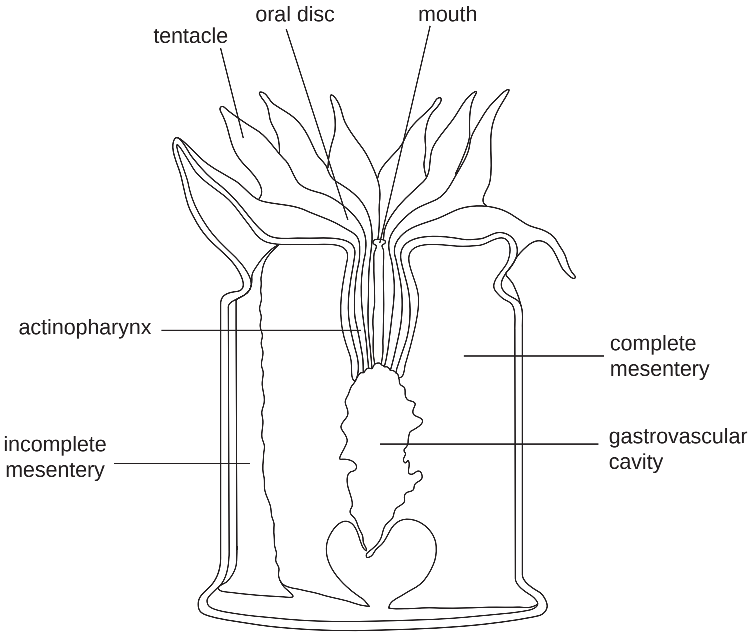

Fig. 3.2. A longitudinal section of a hypothetical anthozoan polyp, showing the characters used in defining the various coral orders. Figure adapted from Bayer and Owre (1968) with permission of Simon & Schuster Inc.

tentacles (Fig. 3.2). Leading downward from the mouth is a tube (the actinopharynx or stomadeum), analogous to the oesophagus, that leads into the main body chamber of the polyp, the gastrovascular cavity (also known as the coelenteron). Except for the stylasterid corals, lamellar sheets of tissue originate from the inside body wall, reaching toward the actinopharynx and also meeting with the undersurface of the oral disc, dividing the polyp into longitudinal

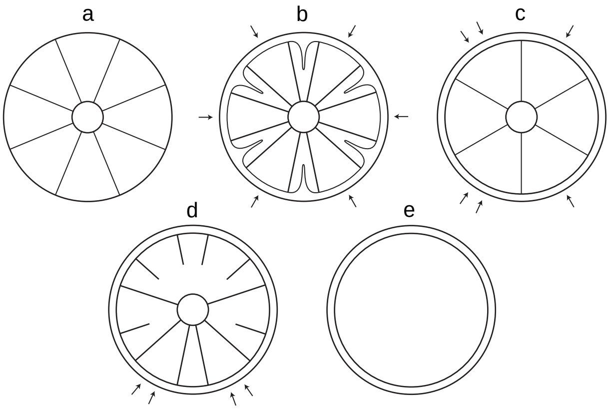

Fig. 3.3. Diagrammatic cross-sections of the polyps of the various coral orders, showing the major differences among them. A double line indicates a hard, usually calcareous, exoskeleton; the central circle represents the mouth and actinopharynx; the radial lines indicate the mesenteries, those reaching to the actinopharynx being complete (or perfect), those falling short being incomplete (or imperfect); arrows indicate regions in which additional mesenteries are formed after the first 6 or 12. (a) Octocorallia, (b) Scleractinia, (c) Antipatharia, (d) Zoanthidea, (e) Stylasteridae.

compartments that are continuous with the hollow tentacles. These sheets, which sometimes occur in pairs, are called mesenteries and are the essence of the coral polyp, carrying digestive cells, the spermacysts and/or oocytes. If the mesenteries reach the actinopharynx they are termed complete (or perfect), if not, incomplete (or imperfect). Another instructive way to visualise the differences among the five coral taxa is diagrammatically as illustrated in Fig. 3.3, which reflects the key characteristics mentioned above.

To summarise, **octocorals** (Fig. 3.3a) have a fixed number of tentacles and complete, unpaired mesenteries, eight in both cases. All octocorals contain tiny calcitic calcium carbonate sclerites in their polyps and branches, and in some cases a flexible internal branch axis composed of proteinaceous gorgonin, and in other cases of solid calcitic or aragonitic calcium carbonate such as in *Corallium* and the bamboo corals (Bayer & Macintyre, 2001). Almost all octocorals are colonial; only one genus is known to be solitary, *Taiaroa* described from New Zealand by Bayer and Muzik (1976). The pinnate arrangement of pinnules on the tentacles is unique to this subclass. Most species are gonochoric and fertilisation may be internal or external.

Scleractinians (Fig. 3.3b) have a variable number of simple tentacles and complete, paired mesenteries, but always the same number of each, which usually occur in multiples of six (e.g. 12, 24, 48, etc.), each new set of mesenterial pairs developing between all previously inserted pairs. Between each mesentery is one simple tentacle and between each mesenterial pair is one aragonitic calcareous septum, usually totalling 6, 12, 24, 48, etc., per polyp. All Recent scleractinians are supported by a robust aragonitic calcium carbonate exoskeleton, which is often diagnostic at the species level. Most shallow-water scleractinians are colonial, whereas most deep-water species are solitary (Cairns, 2007). The hexameral symmetry of mesenteries and calcareous septa is unique to the taxon. Cold-water scleractinians may be either gonochoric or hermaphroditic and more detail on their reproductive ecology is given below, see Section 3.6, p. 100.

Antipatharians (Fig. 3.3c) have 6, 10 or 12 complete, unpaired mesenteries but always a fixed number of 6 simple tentacles. They all have a flexible proteinaceous internal axis that is invariably spiny on its outer surface. All antipatharians are colonial and gonochoric; it is likely that fertilisation is external. Gametes are located only on the two transverse mesenteries. When larvae are ready to settle, they become negatively phototactic and settle in places of low light intensity (D. Opresko, personal communication, 2007). In general, black corals are found in areas of low or no light and where there are strong currents.

Most **zoanthids** (Fig. 3.3d) do not have a skeleton and are thus not considered to be corals, but three species of the genus *Gerardia* develop a dense, proteinaceous, layered axis or encrustation. Like scleractinians, zoanthids have a variable number of tentacles and paired mesenteries; however, the development of the mesenteries of each pair within a polyp is different, the ventral pair both being complete, the dorsal pair both being incomplete, and the other four pairs having a combination of complete and incomplete mesenteries; additional mesenterial pairs are added only adjacent to the ventral pair. Most species are gonochoric but some may be hermaphroditic. Species of *Gerardia* are often bioluminescent when mechanically stimulated.

As hydrozoans, **stylasterids** (Fig. 3.3e) have simpler polyp morphology than anthozoan corals, being composed of a tube with a distal mouth surrounded by a circle of simple tentacles; no internal mesenteries are present. The stylasterid compensates for the lack of mesenteries by having three types of polymorphic zooids: the feeding gastrozooid, the defensive dactylozooid and the reproductive gonophore (also called ampullae). All stylasterids are colonial, the colonies supported by a substantial, often colourful, calcitic or aragonitic exoskeleton (Cairns & MacIntyre, 1992). Most species are gonochoric (Cairns, 1983), fertilisation being internal, the larvae (planulae) developing within discrete ampullar structures embedded in the surface of the skeleton, and eventually released through a small efferent pore (Ostarello, 1973).

Excellent references on the classification, biology and/or physiology of corals include: Hyman (1940), Moore (1956), Bayer and Owre (1968), Dunn (1982), Fautin and Mariscal (1991) and Cairns (2007); as well as the Tree of Life web project: http://tolweb.org/Anthozoa.

3.2 Morphology

Given the logistical problems involved, the interpretation of functional biology of any deep-water organism is fraught with difficulties, and thus only a few have speculated about form and function as it relates to the deep-sea environment. Squires (1967) suggested that the scleractinian family Micrabaciidae adapted to a deep-water environment (some species living as deep as 5000 m) in which calcification was assumed to be more difficult, not by increasing the size of their polyps but by decreasing the weight and density of their skeletons, the latter achieved by corallum porosity, reduction in trabeculae and having thinner corallum elements. Indeed, the skeleton of one of the deepest known scleractinians, *Leptopenus hypocoelus* (Fig. 3.4), is a delicate lattice, and the skeleton constitutes only a small percentage of the coral's weight. Owens (1984) later suggested that the lightness of the micrabaciid skeleton was a pre-adaptation from a shallow-water ancestor that benefited from its light skeleton by being able to move bodily from one place to another. In other words, the Micrabaciidae first gained a selective advantage from their light skeletons because they allowed them to be mobile. Subsequently, the light skeletons pre-adapted them to the deep sea where it is more demanding to produce heavy calcium carbonate skeletons.

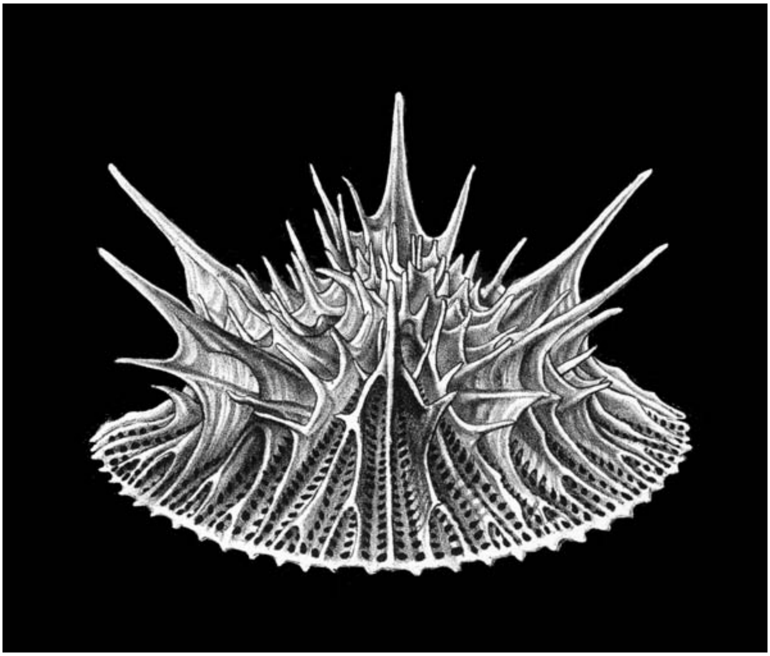

Fig. 3.4. The fragile lattice-like skeleton of the scleractinian coral *Leptopenus hypocoelus* Moseley, 1881, one of the deepest known of the corals. Figure reproduced from Plate 14, Moseley (1881).

In a series of papers, Keller (1978, 1985), Cairns and Keller (1993) and Keller and Pasternak (1996) suggested that the scarcity of food in deep water led to various scleractinian skeletal modifications: (1) a flattened discoidal corallum (e.g. *Stephanocyathus*) to increase the surface area for feeding, (2) highly exsert septa (e.g. *Ulocyathus*) to maximise food capture, (3) a smaller overall size (e.g. the turbinoliids) to reduce the need for food and (4) a lower number of septa. In agreement with Squires (1967), Keller also hypothesised that the skeleton of deep-water scleractinians would be thinner, but that the thinner skeleton could be strengthened by joining adjacent septa directly (e.g. *Deltocyathus*), by transverse synapticulae (e.g. *Fungiacyathus*) or through porous columellas (e.g. dendrophylliids), and by replacing septa with a series of spines (e.g. micrabaciids).

All octocorals contain microscopic calcitic sclerites that occur in great numbers in the branch coenenchyme and polyps. They occur in a bewildering number of shapes and sizes with an equally diverse variety of names; Bayer *et al*. (1983) defined and illustrated 85 types, ranging from the prosaic rod, needle and spindle, to the more poetically named hockeystick, caterpillar, rooted head and finger-biscuit. Lewis and Wallis (1991) have reviewed the form and potential function of some of these sclerite types, concluding that the shape and ornamentation of the various types of sclerites relate to the limitation of movement of adjacent sclerites in various directions, thus in many cases giving rigidity and support as well as flexibility to the branch and polyp.

3.3 Food supply and nutrition

In the previous chapter (Section 2.3, p. 43) we outlined the most significant environmental controls on cold-water corals. These species require appropriate temperatures and salinities, the presence of hard substratum for initial attachment and, importantly, are very often associated with areas of locally enhanced flow regime. Enhanced flows not only remove waste products and limit sediment smothering but also play a crucial role in supplying food to these sessile suspension feeders. In the 1990s another intriguing concept was put forward relating the occurrence of scleractinian cold-water coral reefs to light hydrocarbon seepage that, in some instances, was related to gas hydrate deposits. These ideas effectively stimulated a decade or more of investigations attempting to document gas seepage, notably as a factor important in initiating coral carbonate mound growth and development (see Section 4.4, p. 119).

3.3.1 Gas seeps and the 'hydraulic theory'

The hypothesis that scleractinian cold-water coral reefs were related to light hydrocarbon seepage was first proposed by Hovland (1990) who suggested that the corals were in part feeding on a food chain supported by chemosynthetic bacteria reliant in turn on gas seeps seen in the vicinity of reefs on the Norwegian continental shelf. In a series of subsequent studies (Hovland & Thomsen, 1997; Hovland *et al*., 1998; Hovland & Risk, 2003; Hovland, 2008) this hypothesis was refined and used by Hovland and Mortensen (1999) in the concluding section of their book *Norske Korallrev og prosessor i havbunnen* (*Norwegian Coral Reefs and Seabed Processes*). Here the 'hydraulic theory' is explained by analogy with an oasis in a desert. Just as water brought to the surface by springs in a desert allows life to flourish in an oasis, Hovland and Mortensen suggested that the increased 'hydraulic activity' in the vicinity of a seep could supply inorganic phosphorus, nitrate and sulfur compounds along with organic compounds such as light hydrocarbons (principally methane) creating a chemical milieu that sustains bacterial primary productivity and stimulates a food chain with cold-water corals at the higher trophic levels. In addition, the hydraulic theory predicts, but without clear mechanism, that the increased hydraulic activity created near seeps would promote carbonate production (see discussion of authigenic carbonate production and cold seeps below).

The 1990s also saw the discovery and initial geophysical survey of giant seabed mounds, notably in the Porcupine Basin, northeast Atlantic. Hovland *et al*. (1994a) postulated that structures identified by seismic surveys as potential carbonate 'knolls' or 'bioherms' were related to light hydrocarbon seepage through underlying faults that sustained a bacterial food chain supporting higher trophic groups. Further seismic surveys in the Porcupine Basin led Henriet *et al*. (1998) to conclude that cold-water coral reefs associated with 'carbonate mounds' (see discussion of terminology in Section 4.3, p. 115) might be related to decaying gas hydrate (hydrates form at low temperatures and high pressures and are deposits of a crystalline ice-like substance composed of hydrocarbons, mostly methane, in a rigid case of water molecules). Henriet *et al*. noted that there was no direct evidence that chemosynthetic communities contributed to reef-building, or whether reef-builders preferentially settled and grew on authigenic carbonates found near other active seeps. So far, corroborating evidence to support a direct trophic link between hydrocarbon seepage and cold-water corals has not been found.

The carbon in methane from seeps is dramatically depleted in ^{13}C compared to carbon derived from surface primary production and the δ^{13}C of carbonates precipitated at seep sites can vary between –38‰ and –65‰ PDB, see Topic box 3.1 (Suess *et al*., 1999; Boetius & Suess, 2004). In contrast, skeletal δ^{13}C from *Lophelia pertusa* taken from a variety of settings in the northeast Atlantic ranged between −2.0‰ and −9.9‰ PDB and δ^{13}C from the coral's organic tissue was around –20‰ PDB (Spiro *et al*., 2000; Duineveld *et al*., 2004) comparable to

Topic box 3.1 **Stable isotope ratios and delta notation**

Stable isotopic data are expressed using the delta (δ) notation with abundances given as the ratio of isotopes in the sample compared to that in an international reference standard. For carbon the international standard is the Pee Dee Belemnite (PDB). Oxygen is referenced to Standard Mean Ocean Water (SMOW) and nitrogen is referenced to air. The ratios are expressed as parts per thousand deviation from the standard. So in the case of carbon:

$$\delta^{13}\mathrm{C}_{\mathrm{sample}} = \{(^{13}\mathrm{C}/^{12}\mathrm{C}\ \mathrm{sample})/(^{13}\mathrm{C}/^{12}\mathrm{C}\ \mathrm{standard}) - 1\} \times 1000 \qquad \text{(Eq. 3.1)}$$

shallow-water tropical coral tissues where δ^{13}C values of −14‰ to −22‰ PDB have been reported (Muscatine *et al*., 1989; Yamamuro *et al*., 1995). There is also evidence that the δ^{13}C value of coral animal tissue from zooxanthellate tropical coral species becomes progressively more negative with depth as the corals' reliance on carbon derived from zooxanthellae photosynthesis diminishes and the proportion of allochthonous carbon input, such as demersal zooplankton, increases (Muscatine *et al*., 1989). Interestingly, the δ^{13}C values reported by Muscatine *et al*. from *Agaricia agaricites*, *Montastraea annularis* and *Montastraea cavernosa* collected from 50 m water depth (−16‰ to −22‰ PDB) are broadly equivalent to those reported to date from cold-water corals such as *Lophelia pertusa*. In contrast, Levin and Mendoza (2007) found that mean δ^{13}C values in methane-seep macrobenthos from the Florida Escarpment was −43‰ PDB with samples from species particularly reliant on carbon derived from seeping methane showing δ^{13}C signatures as light as −96‰ PDB. Thus far the carbon isotope signal from cold-water corals does not indicate that they rely on carbon derived from seeping methane. Other nutritional indicators, including δ^{15}N and lipids, discussed below, point to a diet derived from surface primary productivity.

The animals associated with methane seeps often include megafauna that form nutritional symbioses with bacteria. In their review of cold-seep communities, Sibuet and Olu (1998) listed 211 species of which 64 formed chemoautotrophic endosymbioses to derive their energy from methane and/or sulfide oxidation. These chemoautotrophic animals, which have not been found with cold-water coral reefs, include some species of bivalve molluscs from the families Vesicomyidae, Mytilidae, Solemyidae, Thyasiridae and Lucinidae, pogonophoran worms and some species of sponges from the families Cladorhizidae and Hymedesmiidae. For example, the northern Gulf of Mexico is one of the most active hydrocarbon seepage regions known with methane seep-associated communities of chemosynthetic vestimentiferan tubeworms and *Bathymodiolus* mussels (e.g. MacDonald *et al*., 2003). Cordes *et al*. (2008) found little overlap between the fauna with seep-associated vestimentiferan tubeworms and colonies of *Lophelia pertusa* in the Gulf of Mexico, again implying that even in close physical proximity to active hydrocarbon seepage, cold-water corals and their associated fauna are not intimately tied to hydrocarbon seeps. Cold-seep ecosystems are also often characterised by extensive bacterial mats on the seafloor, typically formed by the giant filamentous chemosynthetic species *Beggiatoa* (Larkin *et al*., 1994) and small *Beggiatoa* mats have been photographed during submersible surveys of Scandanavian *Lophelia pertusa* reefs (Hovland & Mortensen, 1999; Hovland, 2005, 2008) but it remains unclear whether these might indicate a seepage site or an anoxic patch caused by local decomposition.

Thus there is little evidence to support the hypothesis that cold-water corals derive nutrition from a seep-based food chain and the characteristic symbiont-containing animals of cold seeps have not been found on cold-water coral reefs. There is some evidence, as in the Gulf of Mexico, that cold-water corals may be located near seepage sites. For example, Sumida *et al*. (2004) reported dredge hauls from seabed pockmarks in the Santos Basin off Brazil that were rich in coral debris and noted that their location could be explained either by a nutritional relationship with seeping hydrocarbons or that the corals benefited from enhanced flow regimes at the edge of the pockmarks. As we discuss below, we believe the current weight of evidence supports the latter explanation. But might methane seeps create local carbonate hardgrounds and provide a suitable settlement substratum for cold-water corals? The focused flow of hydrocarbons supporting microbial communities can lead to localised hardground or ‘chemoherm’ formation (Roberts & Aharon, 1994). Firstly, methane oxidation by sulfate near the sediment surface releases bicarbonate and sulfide to the pore water:

$$CH_4 + SO_4^{2-} \rightarrow HCO_3^- + HS^- + H_2O \qquad \text{(Eq. 3.2)}$$

Secondly, the bicarbonate produced increases alkalinity and brings about calcium carbonate precipitation to form authigenic carbonates, although the precise mechanisms and rates of precipitation remain poorly understood (Luff & Wallmann, 2003):

$$Ca^{2+} + 2HCO_3^- \leftrightarrow CaCO_3 + CO_2 + H_2O \qquad \text{(Eq. 3.3)}$$

Cold-water corals, such as *Lophelia pertusa* in the Gulf of Mexico, can colonise authigenic carbonate outcrops (Schroeder, 2002; Cordes *et al*., 2008). Much debate has focused around whether the initiation of coral carbonate mounds (see Section 4.4.1, p. 120) might be related to hydrocarbon seepage but both indirect seismic studies examining fault patterns beneath the northeast Atlantic Magellan mound province (Huvenne *et al*., 2007) and direct studies based on drilled cores through the Challenger Mound (see Case study 4.1, p. 122) have not found evidence that hydrocarbons were focused to the mounds or produced any evidence that the mounds were initiated on authigenic carbonates (IODP Expedition Scientists, 2005; Williams *et al*., 2006b). Diagenetic studies of hardgrounds from coral carbonate mounds in the northeast Atlantic (Porcupine Seabight and Rockall Bank) confirm that these hardground carbonates are in isotopic equilibrium with seawater ($\delta^{13}C$ is −0.5 to 1.2‰ PDB) and have shown that lithification processes (see Section 4.4.5, p. 130) are probably enhanced by high near-bed current flows (Noé *et al*., 2006). It is to these important enhanced current flows that we now turn.

3.3.2 Hydrography

The earliest observations of cold-water corals noted their association with locally enhanced current regimes, not only drawing the conclusion that such currents supplied food material, but that the presence of cold-water corals indicated where such food material was transported to the seafloor in significant amounts; thus in their 1912 book *The Depths of the Ocean* Murray and Hjort noted that the presence of *Lophelia pertusa* (*Lophohelia prolifera* in those times) was a 'most interesting indication of the motion of the organic matter along the sea-bottom' (cited by Thiem *et al*., 2006). Scandinavian studies in the early and mid-twentieth century frequently noted that reefs of *L. pertusa* were concentrated at fjordic sills or where channels narrowed to speed current flow and enhance food supply (Dons, 1944; Tambs-Lyche, 1958). As our knowledge of cold-water coral occurrence on continental shelves, slopes and seamounts around the world has grown so have efforts to understand the hydrographic regimes of these areas and how they may link surface pelagic production to benthic coral ecosystem consumption.

While there is still relatively little direct information documenting the physical processes by which cold-water coral habitats receive food particles, a growing body of evidence shows that their occurrence can be related to: (1) primary productivity by surface phytoplankton, (2) local hydrographic mechanisms that help deliver both this and secondary zooplankton production to the benthic boundary layer and (3) local flow fields and turbulence regimes that supply both live prey and detrital food particles to the coral fauna. A variety of potential mechanisms has been put forward to explain coral occurrence in different settings. Frederiksen *et al*. (1992) related the occurrence of *Lophelia pertusa* on the upper continental slope around the Faroe Islands and Rockall Plateau, northeast Atlantic, to depths where the slope was critical to semidiurnal internal waves

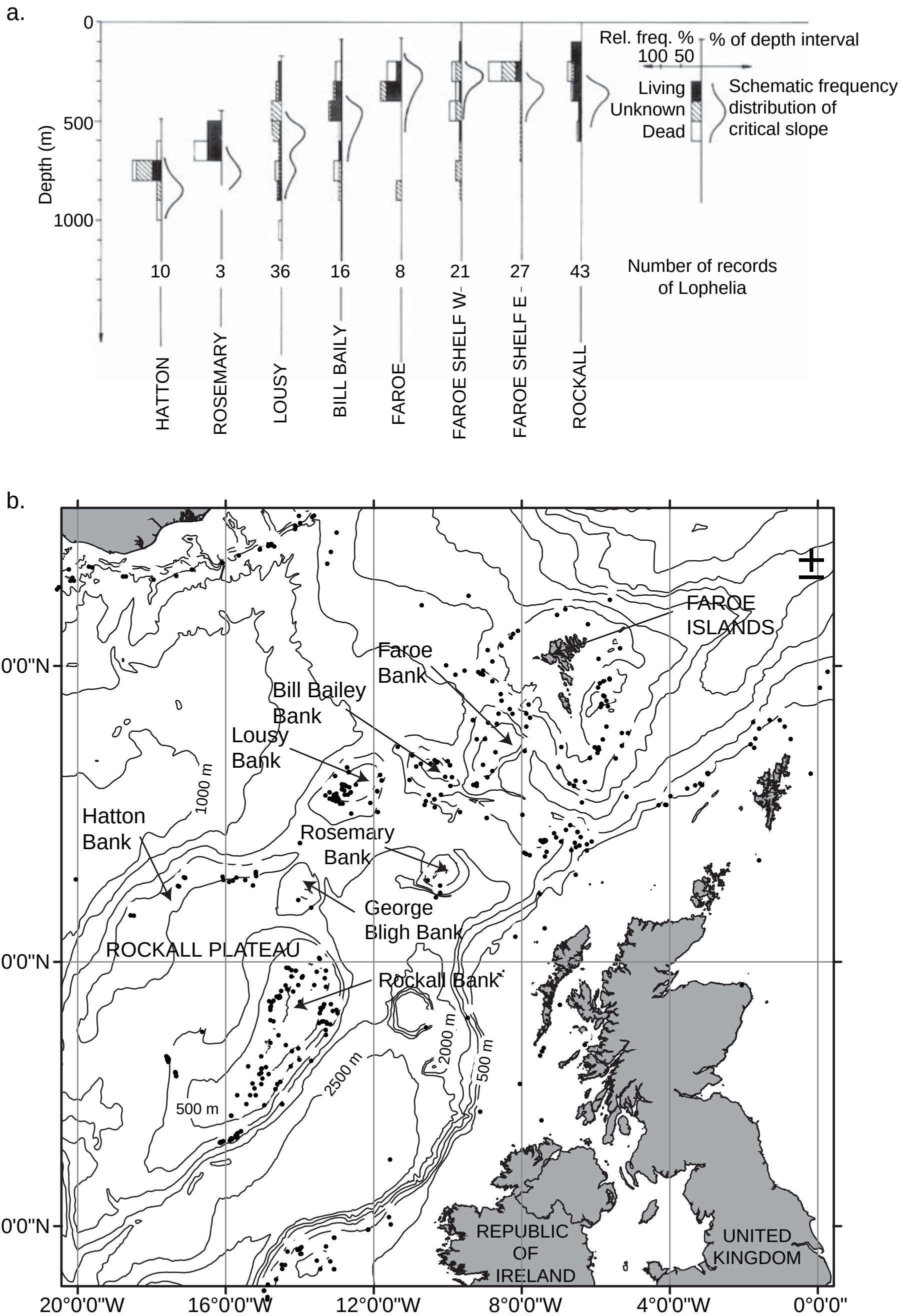

Fig. 3.5. (a) Relationship between depth distribution of coral records (*Lophelia pertusa*) and areas with critical slope for breaking internal waves in the northeast Atlantic. (b) Chart showing location of banks and shelf areas. Figure (a) reproduced from Frederiksen *et al*. (1992) with permission of Taylor & Francis Ltd.

(Fig. 3.5). They postulated two ways in which this might favour coral growth. Firstly, the internal tidal waves would increase vertical nutrient flux through the thermocline and promote phytoplankton production along the shelf edge (New & Pingree, 1990), increasing food flux to shallower populations such as those on the southeastern Faroe Shelf. Their second mechanism helps explain food supply to deeper-dwelling populations, such as those on the Rockall Plateau. At these greater depths, the association between *L. pertusa* and critical slopes is thought to be important because internal waves locally increase mixing at the seabed, resuspending organic particles and spreading this material downslope in particle-rich tongues or nepheloid layers that deliver food to deep-dwelling coral and sponge populations (Klitgaard *et al.*, 1997).

Seamounts and isolated submarine banks project through the water column and can have far-reaching effects on hydrography that can lead to both locally retained circulation patterns, such as Taylor columns, and enhanced flows (White *et al.*, 2007). For example gorgonian and antipatharian corals (notably the antipatharian *Stichopathes*) were much more abundant near current-swept peaks on Jasper Seamount in the Pacific than at equivalent depths on its slopes (Genin *et al.*, 1986). It has recently become clear that such topographic factors are important in understanding coral carbonate mound development around the Rockall and Porcupine Banks in the northeast Atlantic. White *et al.* (1998) demonstrated that cold, nutrient-rich waters formed a 'dome' above Porcupine Bank over the winter months. This nutrient-rich water promotes phytoplankton production in the spring with evidence that the cold, nutrient-rich waters persist until mid-summer. Then, under certain conditions of bottom slope and density stratification, this dense water and retained organic matter may drain slowly downslope through the benthic boundary layer (Ekman drainage) to deliver food particles to the coral carbonate mound coral fauna on the slopes of the bank (White *et al.*, 2005). Related phenomena help to explain the concentration of *Lophelia pertusa* reefs along the Norwegian shelf break. Thiem *et al.* (2006) used a numerical simulation with both an along-slope jet to imitate Atlantic water flow along the shelf and a wind forcing to simulate the common low atmospheric pressure conditions in this region. From this analysis, Thiem *et al.* concluded under both Atlantic inflow and low-pressure simulations that the shelf break, with its concentration of *L. pertusa* reef systems, would receive higher food particle supply than surrounding areas and that particle transfer across the shelf edge could be explained by Ekman transport.

3.3.3 Food particles

We have seen that there is a growing body of work on the hydrographic routes by which primary productivity in the surface levels of the ocean may reach cold-water coral habitats. But what do the corals themselves feed on? Naturally the answer will depend on the coral species in question and, since cnidarians can use diverse food sources from zooplankton to dissolved organic matter, we can anticipate that the answer may also vary spatially and temporally. However, it seems highly likely that species with large individual polyps, like many of the deep reef framework-forming scleractinians, would be better adapted to take large, live prey items than other species, such as those with smaller polyps, which may rely to a greater extent on detrital or even resuspended material. This is akin to Porter's (1976) observations that shallow reef corals with large polyps were best adapted to zooplankton capture while those with small polyps were most suited to light capture and therefore more reliant on carbon translocated from zooxanthellae symbionts (e.g. Davies, 1984; Muscatine *et al*., 1984). Indeed, Porter speculated that azooxanthellate corals would in general have large polyps and long tentacles adapted to capture zooplankton. Observations of live cold-water corals from submersibles and in aquaria seem to bear this out with *Lophelia pertusa* in the field seen to take live calanoid copepods on Norwegian reefs (Freiwald, 2002) and to take both live and dead food material in aquaria (Mortensen, 2001). To date no thorough laboratory feeding trials of the major reef framework-forming scleractinians have been carried out and one-off observations from submersibles cannot give a complete picture of their dietary requirements.

Despite the lack of direct, controlled laboratory studies of feeding, indirect studies of preserved coral material and potential food particles using a variety of nutritional biomarkers are now bearing fruit. Stable carbon isotope studies, summarised above, have not supported any trophic link to light hydrocarbon seepage. Stable nitrogen isotopes provide a classic means of studying trophic status where 3‰ enrichment on average indicates a trophic level in marine food webs (Michener & Schell, 1994), although ^{15}N-enrichment per trophic level may be somewhat less in food-limited deep-sea ecosystems (Iken *et al*., 2001). Duineveld *et al*. (2004) compared δ^{15}N levels between scleractinian reef framework-forming coral tissue from Galicia Bank (northwest Spain) and material sampled by sediment trap. In their analysis, Duineveld *et al*. found that *Lophelia pertusa* and *Madrepora oculata* had similar δ^{15}N values that differed by two trophic levels from phytodetritus sampled at the study site and were close to δ^{15}N values of zooplankton also caught in their sediment trap. In other words, these corals did not appear to feed primarily on algal material but were probably taking a mixed, somewhat omnivorous, diet including zooplankton prey and some algal material. In a subsequent study of trophic structure among the benthic community of coral carbonate mounds on Rockall Bank, northeast Atlantic, Duineveld *et al*. (2007) report similar δ^{15}N values in *L. pertusa* and *M. oculata* and those from other obligate filter feeders (tunicates and bivalve molluscs), implying the corals relied predominantly on the same small particles as the filter feeders.

There is a large literature on food input and carbon flux to the deep sea and three recent review papers are available synthesising information on: (1) carbon flux (Gage, 2003), (2) the seasonally pulsed nature of phytodetrital food-fall (Beaulieu, 2002) and (3) the effects of seasonal variation in organic matter flux on biological processes (Gooday, 2002). Many cold-water corals, notably the structural habitat formers described in Section 2.2, p. 24, are bathyal and will receive a greater proportion of surface production than the estimated 1–3% of primary productivity thought to reach the abyssal seabed (Deuser, 1986). Evidence of annual signals in the growth and reproductive ecology of cold-water corals at high latitudes both point to the probable significance of seasonality in their food supply. Oceanic spring phytoplankton blooms are in turn grazed by zooplankton that produce faecal waste pellets with associated bacterial populations. It is thought that around 90% of this material is recycled within the euphotic zone so only a small fraction is exported to deeper waters. Some of the exported material becomes food for mesopelagic zooplankton and it is possible that the diurnal vertical migration behaviours of some zooplankton are a significant, but as yet unstudied, source of food to bathyal coral populations. Other exported particles tend to aggregate and clump, forming faster falling 'marine snow' capable of sinking at rates of 1–368 m per day (Diercks & Asper, 1997).

There is now evidence that this suspended particulate organic material can remain relatively 'fresh' and lipid rich even at many hundreds of metres depth. Kiriakoulakis *et al*. (2004) used autonomous underwater pumps to sample suspended particulates from the water above the small *Lophelia pertusa* colonies on the Darwin Mounds at almost 1 km depth in the northeast Atlantic. They found that this material was dominated by labile lipids (e.g. polyunsaturated fatty acids) originating mostly from phytoplankton remains and faecal pellets, but with some lipids characteristic of bacteria and microzooplankton. In a subsequent study, Kiriakoulakis *et al*. (2005) compared both δ^{15}N and lipid composition of *Lophelia pertusa* and *Madrepora oculata* in the northeast Atlantic with suspended particulate matter. The corals were enriched in monounsaturated fatty acids including two fatty acids ($C_{20:1}$ and $C_{22:1}$) that are only known to be synthesised by calanoid copepods. Levels of these mesozooplankton markers were significantly higher in the corals than the suspended particulate matter, and higher in *L. pertusa* than *M. oculata*, suggesting that the corals were feeding on mesozooplankton and that *L. pertusa* was perhaps the more carnivorous of the two species; an interpretation supported by heavier δ^{15}N values in *L. pertusa* (Kiriakoulakis *et al*., 2005) and the larger size of its polyps and tentacles. However, it is worth noting that very little is known of cnidarian lipid metabolism and therefore species-specific metabolic, rather than dietary, differences might contribute to the fatty acid variability observed between these two species.

The most detailed study of feeding by cold-water corals with small polyps, typically of octocorals, has been done on polar species from the impressive and diverse suspension-feeding communities found in the freezing waters around Antarctica (see Colour plate 11). For more information on these communities see Gutt and Starmans (1998), Gili *et al*. (2001) and references therein. These feeding studies support the overall interpretation that cold-water octocorals with small polyps typically take small particles with occasional and significant carbon input from larger zooplankton prey. For example, Orejas *et al*. (2003) found that a soft sediment-dwelling bamboo coral (*Primnoisis antarctica*, 200–500 m depth) and a primnoid coral (*Primnoella* sp., 60 – 100 m) found on hard substrata contained very few zooplankton remains. In experimental incubations using live corals with 'natural' plankton concentrations from water collected *in situ*, both species ingested nano- and microplankton but neither species took particles $<5\,\mu m$ in size. *Primnoisis antarctica* preferentially grazed the diatom *Fragillariopsis* spp. but also consumed dinoflagellates and ciliates, and *Primnoella* preferentially consumed dinoflagellates with a small component of ciliates and diatoms. Orejas *et al*. concluded that although zooplankton were probably rare prey items their high carbon content could still make them a significant food source and the ability of these species to ingest small plankton cells, even at low concentrations, might allow them to remain actively feeding for a longer season each year than they otherwise would. The likely diet of other cold-water octocorals has also been investigated using $\delta^{15}N$ to assess trophic status. Sherwood *et al*. (2005a) found that $\delta^{15}N$ levels in gorgonin from *Primnoa* collected from sites ranging from the northeast Pacific, northwest Atlantic, Sea of Japan and South Pacific indicated this octocoral fed mainly on zooplankton and/or sinking particulate matter.

Thus there is now a basis from which our understanding of cold-water coral feeding and nutrition can be developed. There remains a clear need for controlled laboratory studies of feeding mechanisms and rates, but data from both direct studies of octocoral gastric cavity contents and indirect studies using stable isotope and lipid biomarkers support predictions from hydrodynamic studies that cold-water corals are supplied with a diverse range of food from live zooplankton to particle aggregates of marine snow and resuspended material. It will remain important to note that cnidarians are notoriously cosmopolitan consumers (Anthony & Fabricius, 2000) adapted on a continuous spectrum from photo-autotrophic symbiosis at one extreme, through species that feed on algal, detrital and dissolved organic matter, to carnivorous predators at the other extreme. Some cold-water soft corals, such as the Antarctic nephtheid *Gersemia antarctica*, are even able to slowly bend and deposit feed on the seabed (Slattery *et al*., 1997).

Finally, the likely importance of zooplankton prey is highlighted not just in studies of the large-polyped reef framework-forming scleractinians, but also in studies of Antarctic gorgonian corals. It seems probable that cold-water corals will benefit from regular, short 'feeding frenzies' associated with vertical plankton migration such as the diurnal zooplankton migration and retention recorded over a seamount in the Gulf of California (Valle-Levinson *et al*., 2004) or over longer, seasonal periods they may get opportunities to feed from overwintering zooplankton populations that migrate to deeper waters (e.g. *Calanus finmarchicus* copepods in the North Atlantic, Hind *et al*., 2000). Once again, the significance of these potentially important routes of food input to cold-water coral habitats has not yet been studied.

3.4 Growth rates

Determining the age and growth rates of deep-water organisms is fraught with difficulties; they are inaccessible, frequently slow-growing and often hard to culture in the laboratory, where in any case it is hard to create conditions to reflect those in the field. The earliest information on cold-water coral growth came in the late nineteenth century from observations of scleractinians that had colonised trans-Atlantic telegraph cables (Duncan, 1877). More recently, these records have been supplemented with observations from other man-made structures and great progress has been made in understanding cold-water coral age and growth by using geochemical analysis of skeletal isotopes in relation to visual growth banding patterns. Table 3.2 summarises studies that have reported growth rates of cold-water corals.

Growth estimates have typically been reported either in terms of linear extension or radial thickening of the coral skeleton. Linear extension rates, often reported from scleractinians, give an idea of how high a colony may develop above the seafloor over time. In contrast, radial thickening estimates are most commonly reported from the stems of gorgonian, zoanthid and antipatharian corals. Considerable recent efforts have gone into studying radial growth patterns from these groups because their long life spans and the tree ring-like banding of their skeletons in cross-section make them valuable sources of palaeoceanographic information derived from a variety of geochemical proxies (see Chapter 7).

Linear extension estimates have been taken in a variety of ways each having its own benefits and drawbacks. The simplest and most direct approach has been to measure the length of coral growth on man-made structures of a known age. However, since the corals settled at some unknown time after the structures were put in place growth rates derived in this way will always be underestimates. Despite this, direct observations from man-made structures give a valuable

Table 3.2 *Growth rates of cold-water corals.*

Order	Species and depth	Growth rate (mm yr^{-1})	Growth parameter and method	Reference
Scleractinia	*Desmophyllum cristagalli* (= *D. dianthus*)	0.5–2.0	Linear extension from ^{226}Ra/^{210}Pb radionuclide decay technique	Adkins *et al.* (2004)
	Desmophyllum cristagalli (= *D. dianthus*)	0.5–1.0	Linear extension from coupled U/Th and ^{14}C dating	Risk *et al.* (2002)
	Desmophyllum cristagalli (= *D. dianthus*) (421–2180 m)	0.1–3.1	Linear septal extension from U/Th dating	Cheng *et al.* (2000)
	Enallopsammia rostrata (1410 m)	5.0	Linear extension from ^{226}Ra/^{210}Pb radionuclide decay technique	Adkins *et al.* (2004)
	Lophelia pertusa (955–1006 m)	7.0	Linear extension from sample from man-made structure of known age	Duncan (1877)
	Lophelia pertusa (800 m)	6.0	Linear extension from sample from man-made structure of known age	Wilson (1979)
	Lophelia pertusa (300 m)	25.0	Linear extension from apparently annual cycles of C/O stable isotopes	Mikkelsen *et al.* (1982)
	Lophelia pertusa (250 m)	19.0	Linear extension from apparently annual cycles of C/O stable isotopes	Freiwald *et al.* (1997a)
	Lophelia pertusa (200–350 m)	6.0	Linear extension from apparently annual cycles of C/O stable isotopes	Mortensen & Rapp (1998)
	Lophelia pertusa (60–109 m)	26.0	Linear extension from sample from man-made structure of known age	Bell & Smith (1999)
	Lophelia pertusa (100 m)	5.0	Linear extension from sample from man-made structure of known age	Roberts (2002)
	Lophelia pertusa (94–115 m)	19.0–34.0	Linear extension from sample from man-made structure of known age	Gass & Roberts (2006)
	Lophelia pertusa (214–218 m)	15.0–17.0	Linear extension from live coral grown in aquaria	Orejas *et al.* (2008)

	Madrepora oculata (214–218 m)	3.0–18.0	Linear extension from live coral grown in aquaria	Orejas *et al.* (2008)
	Enallopsammia rostrata (1410 m)	0.07	Radial growth from ^{226}Ra/^{210}Pb radionuclide decay technique	Adkins *et al.* (2004)
Gorgonacea	*Calcigorgia spiculifera* (18–29 m)[a]	-4.3–19.2	Linear extension from video records of tagged colonies	Stone & Wing (2001)
	Corallium secundum (350–475 m)[b]	9.0	Linear extension from assumed annual radial growth rings	Grigg (1976, 2002)
	Primnoa pacifica (< 200 m)[c]	17	Linear extension from ^{210}Pb decay and visual growth rings	Andrews *et al.* (2002)
	Primnoa resedaeformis (450 m)	1.5–2.5	Linear extension from ^{14}C dating and comparison with live specimens	Risk *et al.* (2002)
	Primnoa resedaeformis (262–542 m)	17	Linear extension from colony height and assumed annual growth bands	Mortensen & Buhl-Mortensen (2005)
	Corallium niobe (640 m)	0.13	Radial growth from ^{14}C dating	Griffin & Druffel (1989)
	Corallium niobe (600 m)	0.11	Radial growth from ^{210}Pb decay and ^{14}C dating	Druffel *et al.* (1990)
	Corallium rubrum (15–62 m)	0.18	Radial growth from growth rings in calcein-stained organic matrix	Marschal *et al.* (2004)
	Corallium secundum (450 m)	0.17	Radial growth from ^{14}C dating	Roark *et al.* (2006)
	Corallium sp., possibly *C. regale* (1482 m)	0.043	Radial growth from ^{210}Pb decay	Andrews *et al.* (2005)
	Unidentified Isididae (700 m)	0.05–0.16	Radial growth from ^{14}C dating and visual growth rings	Roark *et al.* (2005)
	Keratoisis sp. (1000 m)	0.05	Radial growth from ^{210}Pb decay and U/Th dating	Thresher *et al.* (2004)
	Keratoisis sp. (1000 m)	0.11	Revised radial growth estimate of Thresher *et al.* (2004)	Thresher *et al.* (2007)

Table 3.2 (*cont.*)

Order	Species and depth	Growth rate (mm yr^{-1})	Growth parameter and method	Reference
	Mid-Holocene fossil *Keratoisis* sp. (680 m)	0.2	Radial growth from ^{14}C dating and growth rings	Noé *et al.* (2008)
	Keratoisis sp. (935 m)	0.22	Radial growth from growth rings and ^{210}Pb decay	Tracey *et al.* (2007)
	Lepidisis spp. (690–1030 m)	0.15–0.32	Radial growth from growth rings and ^{210}Pb decay	Tracey *et al.* (2007)
	Primnoa pacifica (<200 m)[c]	0.18	Radial growth from ^{210}Pb decay and visual growth rings	Andrews *et al.* (2002)
	Primnoa pacifica (350–505 m)	0.12	Radial growth from assumed annual growth rings	Matsumoto (2007)
	Primnoa resedaeformis (262–542 m)	<0.5	Radial growth from assumed annual growth rings	Mortensen & Buhl-Mortensen (2005)
	Primnoa resedaeformis (450 m)	0.044	Radial growth from ^{14}C dating	Risk *et al.* (2002)
Zoanthidae	*Gerardia* sp. (380–410 m)[b]	66.0	Linear extension from assumed annual growth rings	Grigg (1976, 2002)
	Gerardia sp. (620 m)	~0.005–0.02	Radial growth from ^{14}C dating	Druffel *et al.* (1995)
	Gerardia sp. (400–450 m)	0.014–0.045	Radial growth from ^{14}C dating	Roark *et al.* (2006)
Antipatharia	*Antipathes dendrochristos* (106 m)	15	Linear extension from dated colony (140 y) assuming total height of 2.1 m	Love *et al.* (2007)
	Antipathes dichotoma (~50 m)[d]	64.2	Linear extension from tagged colonies over 3.5 years	Grigg (1976)

Antipathes grandis (~50 m)[d]	61.2	Linear extension from tagged colonies over 3.5 years	Grigg (1976)
Antipathes dendrochristos (106 m)	0.121	Radial growth from growth rings, ^{210}Pb decay and ^{14}C dating	Love *et al.* (2007)
Antipathes dichotoma (50 m)[d]	0.13–1.114	Radial growth from ^{14}C dating	Roark *et al.* (2006)
Leiopathes glaberrima (450 m)[e]	$\leq$0.010	Radial growth from ^{14}C dating	Roark *et al.* (2006)
Leiopathes glaberrima (307–679 m)	0.015	Radial growth from ^{210}Pb decay and visual growth rings	Williams *et al.* (2006a)

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[a] Negative growth rates may have been an artefact of the measurement technique (Stone & Wing, 2001).

[b] Growth rate appears overestimated by incorrect assumption that growth rings are annual (Roark *et al.*, 2006).

[c] Published as *Primnoa resedaeformis* but genus since revised by Cairns and Bayer (2005). Depth from Risk *et al.* (2002).

[d] These relatively shallow corals live in warmer waters and probably receive greater food supply explaining higher growth rates (Roark *et al.*, 2006).

[e] Growth rate varied with faster growth when coral was younger (Roark *et al.*, 2006).

context to compare indirect growth estimates derived from stable isotope cycles or radioisotope decay.

Stable isotopes of carbon and oxygen are strongly correlated in azooxanthellate scleractinian corals (see Section 7.1.2, p. 218 for more discussion) and cycles in the proportions of these isotopes have been inferred to relate to differences in calcification rate over the course of seasonal cycles at the high latitudes where these corals were growing. For example, in the northeast Atlantic estimates of linear extension in *Lophelia pertusa* derived from these apparently annual cycles in C and O stable isotopes vary from 6 to 25 mm yr^{-1} (Mikkelsen *et al.*, 1982; Freiwald *et al.*, 1997a; Mortensen & Rapp, 1998) within the range of 5 to 34 mm yr^{-1} from direct estimates based on man-made structures (Duncan, 1877; Wilson, 1979; Bell & Smith, 1999; Roberts, 2002; Gass & Roberts, 2006) and the 15 to 17 mm yr^{-1} recently estimated from *L. pertusa* in aquaria (Orejas *et al.*, 2008).

3.4.1 Growth bands and chronologies

A number of cold-water corals, notably the precious, primnoid and bamboo corals (Gorgonacea), the gold coral *Gerardia* (Zoanthidae) and the black corals (Antipatharia), lay down growth bands that can be seen in cross-sections of their trunk-like stems (Fig. 3.6). Counting these growth bands, akin to tree rings, can be used to estimate age and growth rate, but only if the chronology of banding is established. A

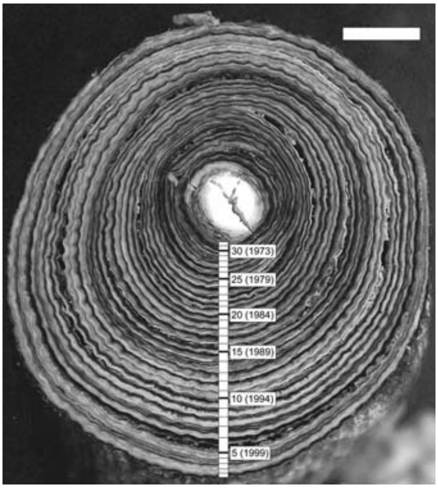


Fig. 3.6. Cross-section of the gorgonian *Primnoa resedaeformis* showing white central rod and clear growth banding of the horny axis produced between the early 1970s to 2001 when this coral was collected (scale bar 2 mm). Figure reproduced from Sherwood *et al.* (2005c) with permission of Inter-Research.

particularly powerful approach is to combine visual growth bands with chronologies verified by independent dating techniques. For example, Andrews *et al.* (2002) validated annual growth bands in the gorgonian *Primnoa pacifica* (published as *P. resedaeformis* before revision by Cairns and Bayer (2005)) from the Pacific by measuring ^{210}Pb decay over the length of a colony and Sherwood *et al.* (2005c) used the ^{14}C signal from atomic bomb tests as a time marker to verify that bands counted in *P. resedaeformis* from the Atlantic were also formed annually (Fig. 3.7).

These techniques, notably ^{210}Pb dating, have proved particularly successful when applied to bamboo and black corals (see Table 3.2). Lead-210 is incorporated into the coral skeleton as it grows from where it decays with a half-life of 22.3 years. By recording ^{210}Pb levels in samples from the inner, older portions to the outer, younger portions of a coral in cross-section it is possible to estimate the coral's age and infer its radial growth rate. Lead-210 dating works well to approximately 100 years of age after which ^{210}Pb activity decreases to approach that of ^{226}Ra (in other words the ratio of ^{210}Pb:^{226}Ra must exceed 1.0 indicating sufficient ^{210}Pb is present for this technique to be viable). However, one disadvantage of ^{210}Pb is that it requires relatively large sample sizes hindering fine-scale analysis and limiting temporal resolution.

Uranium–thorium dating (also referred to U/Th, uranium-series disequilibrium, uranium-series or thorium-230 dating) relies on assessing the degree to which

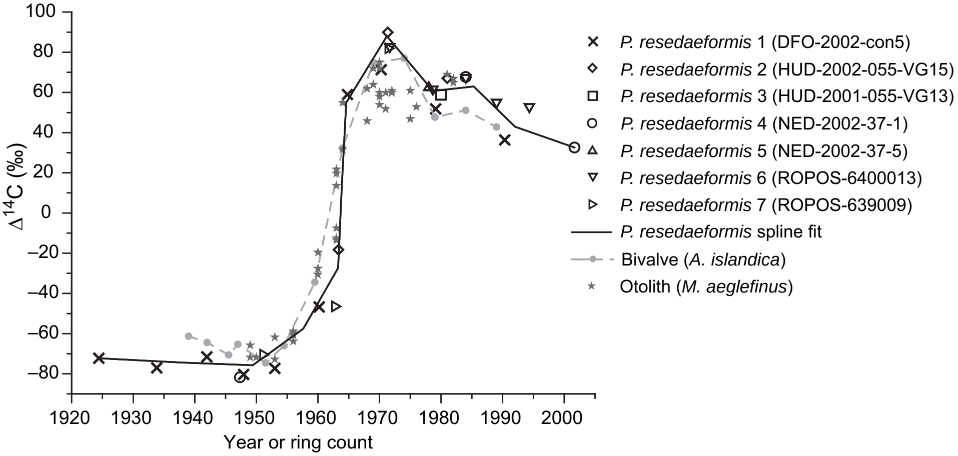


Fig. 3.7. The gorgonian *Primnoa resedaeformis* clearly reproduces the bomb Δ^{14}C curve (see Fig. 3.9). Here the data from seven colonies collected in the northwest Atlantic are shown together with data for comparison from the bivalve *Arctica islandica* and otoliths from *Melanogrammus aeglefinus*. The corals were collected from depths 250-475 m in the Northeast Channel (Atlantic Canada, northwest Atlantic). Sample numbers are given in parentheses. Figure redrawn from Sherwood *et al.* (2005c) with permission of Inter-Research.

^{234}U and its daughter isotope ^{230}Th have reached equilibrium. In simple terms, since uranium is soluble in seawater whereas thorium is largely not, this approach assumes any thorium isotopes derived from uranium in a coral skeleton have come from uranium incorporated while the coral was growing. Uranium–thorium dating has been used extensively since the late 1960s (Broecker *et al*., 1968; Mesolella *et al*., 1969) to date shallow-water corals and follow sea-level changes (e.g. Cutler *et al*., 2003). However, thorium reaches higher concentrations in deep ocean waters and careful cleaning and sample preparation are needed to ensure U/Th dates reflect closed system decay within the coral skeleton and not isotopes incorporated in secondary precipitates (Cheng *et al*., 2000). The radioactive decay of ^{234}U to ^{230}Th has a half-life of 245 000 years and U/Th dating can be used over time periods extending back approximately 500 000 years before present.

It is important to note that all available dating approaches have benefits and drawbacks associated with them. Lead-210 dating requires relatively large amounts of material, but provides good chronologies for live-collected corals with life spans of within 100 years or so. On the other hand, U/Th dating works most reliably to determine when sub-fossil specimens lived, on time periods of thousands to tens of thousands of years before present.

While data on cold-water coral growth rates remain relatively sparse, and direct studies of calcification rates have not been completed, some overall trends are apparent. As might be predicted, there is evidence that corals in deeper waters, further removed from surface production, grow more slowly than those in shallower waters closer to the euphotic zone (Fig. 3.8). This trend is apparent for both linear extension and radial thickening estimates, with a particularly clear trend evident from *Corallium* species where five independent studies using a variety of methods show a clear and largely linear decline in radial growth rate with depth (Fig. 3.8d). However, there has been little work to date on environmental growth controls. Recently Matsumoto (2007) suggested that *Primnoa pacifica* from the Shiribeshi Seamount in the cold waters (0.6−0.7°C) of the Sea of Japan grew more slowly than the same species in the warmer waters (5−8°C) of the northeast Pacific (Andrews *et al*., 2002 and see data in Table 3.2). However, it is important to note that as well as the temperature differences the individuals sampled by Matsumoto were from slightly greater depths (350−505 m) than those sampled by Andrews *et al*. (<200 m) and may have experienced different levels of food input.

Thus, despite observations of cold-water coral growth extending back over a century and recent studies showing their strengths as palaeoceanographic archives (see Chapter 7), our understanding of growth and calcification rates remains at best rudimentary. These gaps in our knowledge constrain our ability to

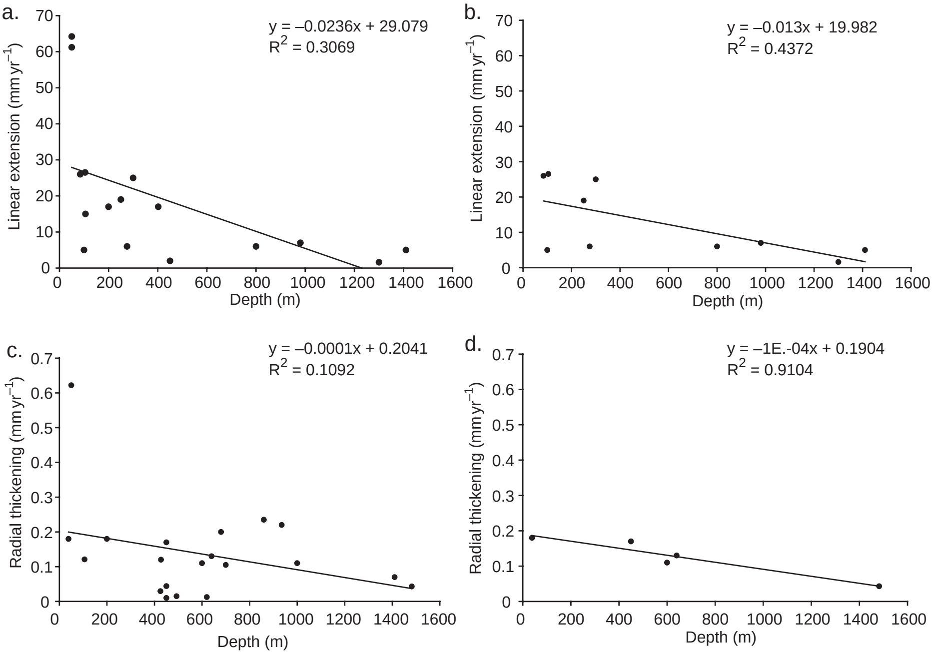


Fig. 3.8. Relationship between cold-water coral growth rates and water depth: (a) linear extension rates for all species, (b) linear extension rates for Scleractinia, (c) radial thickening rates for all species, (d) radial thickening rates for *Corallium*. Table 3.2 summarises data sources. Where growth rates are given as ranges the median of the range is plotted. Lines illustrate linear regressions for these data with equations for each line shown. The rapid growth rates for a few of the shallowest specimens shown in (a) and (c) suggests that growth may exponentially decline with depth. More data are needed to examine this in detail.

understand the palaeorecords and are particularly worrying given the predictions of climate models that the carbonate chemistry and temperatures of the world's oceans will change rapidly in the coming years (see Section 8.1.4, p. 247).

3.4.2 Longevity and carbon sources

Chapter 4 will describe the longevity of cold-water coral reefs and mound structures and Chapter 5 will discuss the importance of this highly complex deep-water structural habitat. The longest-lasting cold-water coral structures are without doubt the reef frameworks formed by the scleractinian coral species described in Section 2.2.1, p. 25. But just as the skeletal remains of reef framework-forming scleractinians can form long-lasting structural habitat, some groups of cold-water corals are themselves very long-lived and provide not only important habitat but a valuable archive of past environmental conditions in their skeletal chemistry (see Chapter 7).

The longest-lived marine organisms are cold-water corals with recent work showing that the oldest examples have been alive since before the time Tutankhamun ruled in ancient Egypt (1333 BC–1322 BC). Druffel *et al.* (1995) were among the first to note the great longevity of cold-water corals by using ^{14}C dating to estimate the age of the gold coral *Gerardia* (see Colour plate 9) collected live from 620 m depth off Little Bahama Bank in the Atlantic. This *Gerardia* sample was ^{14}C dated to 1800 years prompting Druffel *et al.* to refer to it as the 'bristlecone pine of the deep sea'. Carbon-14 dating is often associated with archaeological studies since carbon is ubiquitous in bone, wood and ash remains of past civilizations and the half-life of radioactive ^{14}C, 5730 years, makes its exponential decay a chronometer over the timescales of human history. But to use ^{14}C dates from a living organism one must understand both the organism's carbon sources and the ^{14}C age of these sources. In the case of cold-water corals this means understanding the carbon sources for their skeletons, both the calcium carbonate and, in the case of octocorals, antipatharians and gold corals, the organic components. However, one great advantage of using ^{14}C dating to age cold-water corals and follow their growth rates is that one can use the spike in ^{14}C from atomic bomb testing beginning in the late 1950s and early 1960s as a unique time marker (Fig. 3.9).

Roark *et al.* (2006) demonstrated that it is possible to discriminate carbon sources and age cold-water corals using ^{14}C dating techniques and the chronology developed from bomb ^{14}C time markers. For example, the ^{14}C ages of the outermost, recently deposited skeleton of proteinaceous *Gerardia* corals sampled from Hawaiian seamounts corresponded with the age of surface waters implying that recently exported particulate organic carbon was the main source for this organic skeleton formation. In contrast, ^{14}C results from the calcareous precious coral *Corallium secundum* taken from the same sites as the *Gerardia* corals, were similar to those from dissolved inorganic carbon (DIC) in seawater. This implies *C. secundum*, like other calcareous cold-water corals, uses DIC as a primary source of carbon for calcium carbonate production (see Section 7.1, p. 211). This information allowed Roark *et al.* to interpret the ^{14}C ages to give life spans for their *C. secundum* specimens of 71 years as opposed to estimates of 29 years derived using an earlier growth ring count method that incorrectly assumed visual growth rings were annual (Grigg, 1976, 2002; see Section 8.1.5, p. 251). Mirroring the long life spans reported by Druffel *et al.* for Atlantic *Gerardia*, Roark *et al.* report that Pacific *Gerardia* were over 800 years old when collected with the longest-lived coral in their study, the antipatharian *Leiopathes glaberrima*, estimated to be 2320 years old (note the genus *Leiopathes* is undergoing taxonomic revision). More recent analysis shows that *Leiopathes* corals may live for over

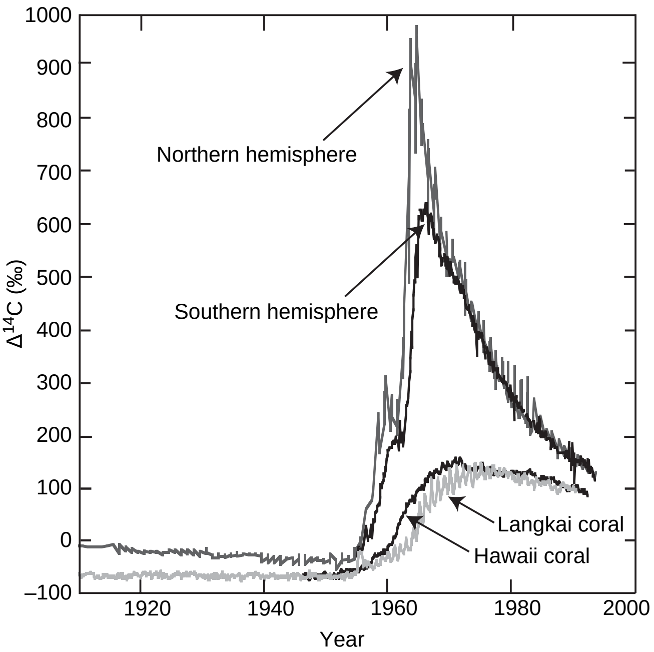


Fig. 3.9. Graph showing rapid increase in ^{14}C from atomic weapons testing in surface waters from both the northern and southern hemispheres (Levin *et al.*, 1994; Manning & Melhuish, 1994; Levin & Kromer, 1997). Shortly after this pulse, increased ^{14}C was detected in shallow-water tropical corals from Hawaii (T. Guilderson, unpublished data) and Langkai, Makassar Strait, Indonesia (Fallon & Guilderson, 2008) in the Pacific. This pulse of ^{14}C provides a useful time marker that helps develop growth chronologies in corals and other marine organisms. $\Delta^{14}C$ is the $^{14}C/^{12}C$ ratio, given as the ratio of the sample to the pre-industrial and pre-atomic bomb standard. The overall magnitude and temporal offsets between the maximum peaks in the atmospheric and surface ocean curves result from the mixing of older marine water and water recently ventilated with the atmosphere. Figure courtesy of S. Fallon and T. Guilderson.

4000 years (B. Roark, personal communication, 2008) making them, by some margin, among the longest-lived animals on Earth.

The most striking examples of how cold-water corals can utilise different carbon sources comes from deep-sea octocorals that have both organic gorgonin and inorganic calcareous components in their skeletons. This is most obvious in the bamboo corals (family Isididae) which have a characteristic two-part skeleton of calcareous internodes, joined by short flexible organic nodes consisting of the black scleroprotein ‘gorgonin’. Figure 3.10 illustrates the difference in $\Delta^{14}C$ between the calcareous and organic components of a bamboo coral showing that carbon used in the calcareous internodes was derived from dissolved inorganic carbon at depth, whereas the carbon in the organic nodes and coral tissue matched the $\Delta^{14}C$ values of

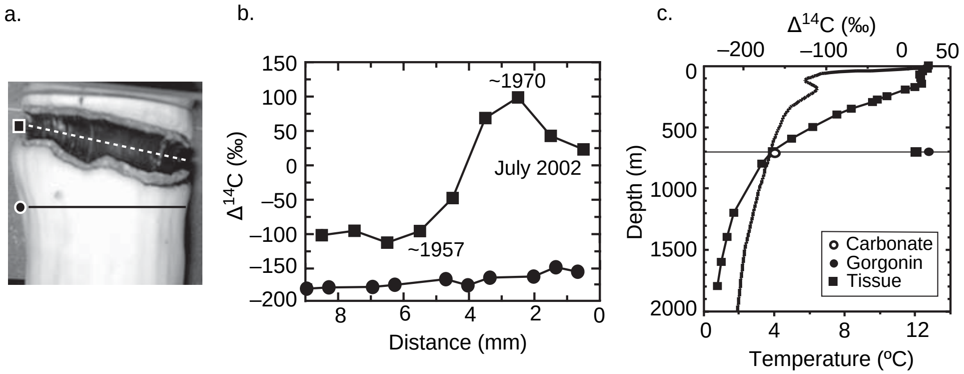


Fig. 3.10. Gorgonian bamboo corals incorporate carbon from seawater dissolved inorganic carbon (DIC) into the calcium carbonate internodes and carbon from particulate organic carbon into their gorgonin nodes. (a) Photograph of bamboo coral showing direction of radial transects across a gorgonin node (dotted line, square symbol) and a carbonate internode (solid line, round symbol). (b) Δ^{14}C measurements from these two transects showing distinctive bomb ^{14}C curve from the gorgonin node (square symbols) compared with the measurements from the calcitic skeleton (round symbols). (c) Δ^{14}C (connected square symbols) and temperature (continuous line) profiles versus depth showing bamboo coral carbonate internodes plotting with seawater DIC whereas gorgonin nodes and coral tissue both plot with surface Δ^{14}C values. Figures redrawn from Roark *et al.* (2005), © 2005 American Geophysical Union, with permission of the American Geophysical Union.

surface waters implying they were synthesised from recently exported particulate organic carbon, effectively the food the coral was eating (Roark *et al.*, 2005). This pattern has also been reported from *Gerardia*, as described above (Griffin & Druffel, 1989; Druffel *et al.*, 1995; Roark *et al.*, 2006), the gorgonians *Primnoa resedaeformis* (Heikoop *et al.*, 2002; Sherwood *et al.*, 2005c), *Paragorgia johnsoni* (Griffin & Druffel, 1989) and *Corallium niobe* (Griffin & Druffel, 1989).

As discussed earlier in this chapter, cold-water corals appear tightly coupled to food sources in the surface ocean and using Δ^{14}C to follow carbon sources of cold-water corals reinforces this close relationship. Radiometric and direct growth observations are beginning to help us understand coral longevity and growth rates. However, as we discuss below, our understanding of how cold-water corals function physiologically remains limited, largely because of the technical challenges of sampling live animals to study their physiology.

3.5 Ecophysiology

Corals, in common with the rest of the phylum Cnidaria, are relatively simple animals composed of two cellular layers, an ectoderm (or epidermis) facing the

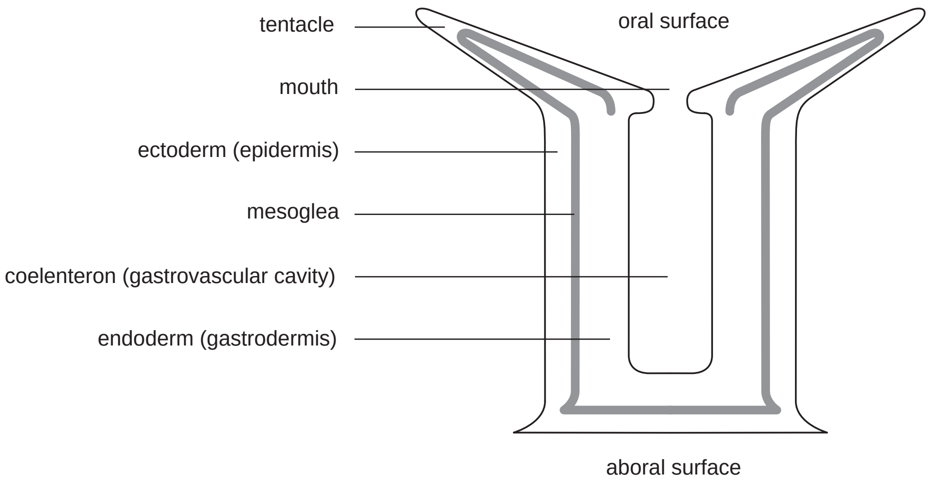


Fig. 3.11. Simplified schematic of a coral polyp to illustrate its two cell layers; the outer ectoderm and inner endoderm separated by a gelatinous mesoglea.

outside world and an endoderm (or gastrodermis) that faces the polyp's internal body cavity, the gastrovascular cavity or coelenteron (Fig. 3.11). These two cell layers are separated by a gelatinous mesoglea – a feature best developed in the Scyphozoa where the mesoglea forms the jelly of the jellyfish. As described earlier in this chapter, cold-water coral polyps, apart from the stylasterids, contain mesenteries in mirror-image pairs. The mesenteries are protected within the coelenteron where food is digested and absorbed. Corals do not have true reproductive organs, rather the gametes (oocytes and spermatocysts) develop in the acellular mesoglea. Mature gametes (or larvae in the case of brooding species) are released into the coelenteron, and from there into the surrounding water, where eggs are fertilised and larvae develop, see Section 3.6, p. 100 on coral reproduction below. Thus despite being considered among the more simple metazoans without differentiated organs, the Cnidaria do have tissues that are specialised for certain roles such as gamete development and muscular contraction. However, without respiratory and excretory organs, gaseous exchange and excretion must take place across these cell layers to and from the surrounding water. Although cnidarians, such as the sticholodactylid sea anemones and large scyphozoans, can reach considerable sizes they remain essentially water-filled bags where the live cell layers are never far removed from seawater and upper size limits are presumably imposed by diffusion. Much of what we understand about cnidarian physiology comes from studies of sea anemones, probably because anemones are ubiquitous, accessible and relatively easy to culture in aquaria. An excellent and detailed account of the functional biology of sea anemones is given by Shick (1991).

3.5.1 Respiratory physiology

Following the pioneering studies of Yonge *et al.* (1932) on the Great Barrier Reef, zooxanthellate tropical coral respiration has been intensively studied in large part to understand the contribution of photosynthesis by endosymbiotic zooxanthellae to coral host nutrition (e.g. Davies, 1984; Muscatine *et al.*, 1984). This body of work now provides a context to help interpret stresses on tropical coral ecosystems, which range from elevated temperatures (causing coral ‘bleaching’ from the expulsion of zooxanthellae) to ocean ‘acidification’ caused by the perturbations in seawater carbonate chemistry from anthropogenic carbon dioxide emissions (Hoegh-Guldberg *et al.*, 2007). At the time of writing only one study on the ecophysiology of a reef framework-forming cold-water coral had been published. By collecting *Lophelia pertusa* from the relatively shallow inshore Mingulay reef complex in the northeast Atlantic, Dodds *et al.* (2007) were able to maintain this framework-forming scleractinian live in aquaria to study the coral’s respiratory physiology using closed chamber respirometry. *Lophelia pertusa* showed some ability to maintain its respiration rate over a range of pO_2 between 10 and 20 kPa, perhaps by expanding its polyps as ambient oxygen levels dropped. Interestingly, *L. pertusa* survived periods of up to 96 hours under hypoxia (pO_2 approximately 2 kPa) and showed significantly enhanced respiration rates when returned to normoxia after one hour exposure to anoxic conditions, both results pointing to some capacity for anaerobic metabolism. But perhaps the most striking finding of this study was the very marked effect small changes in ambient temperature had on this coral’s metabolic rate. Working within the normoxic range (16–21 kPa) and using experimental temperatures within the seasonal range recorded in the field (6.5–11°C), Dodds *et al.* showed that the rate of oxygen consumption increased three-fold from the colder to warmer treatments (Fig. 3.12) and derived Q_{10} values using the van’t Hoff equation:

$$Q_{10} = (k_2/k_1)^{10/(t_2-t_1)} \qquad \text{(Eq. 3.4)}$$

where k_1 and k_2 are the rates of oxygen consumption corresponding to low temperature (t_1) and high temperature (t_2), respectively.

A Q_{10} value gives the factor by which a reaction, in this case an animal’s respiration rate, would increase if it were subjected to a 10°C temperature increase. The Q_{10} values from *L. pertusa* all exceeded the typical value of two for biochemical and physiological processes implying that this species was notably sensitive to temperature change (a reflection of field observations suggesting it is restricted to a relatively narrow temperature range of 4–11°C). A corollary of this would be that if a sustained environmental temperature increase were not

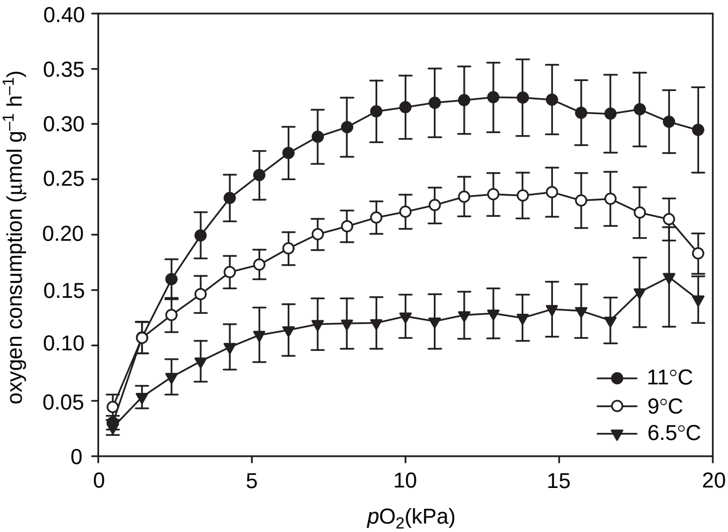


Fig. 3.12. The relationship between the mean rate of oxygen consumption ($\pm$SE) of *Lophelia pertusa* and oxygen partial pressure (pO_2) at three different temperatures (6.5°C, 9°C and 11°C). Data normalised to live coral buoyant weight. Figure reproduced from Dodds *et al.* (2007), with permission of Elsevier.

accompanied by an equivalent increase in food supply then metabolic requirements might outstrip supply. Potential implications of climate change on cold-water corals are discussed in Section 8.1.4, p. 247. This laboratory study of respiratory physiology also shed light onto the possible significance of oxygen as one of a suite of environmental variables controlling cold-water coral distribution (see Section 2.3, p. 43). Figure 3.12 shows that at 9°C the respiration rate of *L. pertusa* starts to decline markedly between 9–10 kPa, equivalent to an oxygen concentration of approximately 3.3 ml l^{-1} at the Mingulay reef complex (salinity 35, temperature 9°C). This matches well with the lower limit of oxygen levels (3–5 ml l^{-1}) that correspond to areas where *L. pertusa* had been recorded in the northeast Atlantic (Freiwald, 2002) and to spatial habitat modelling suggesting that *L. pertusa* would not be found in dissolved oxygen levels less than 4.3 ml l^{-1} (Davies *et al.*, 2008), see Section 5.6, p. 168.

3.5.2 *Excretion and osmotic balance*

Just as gaseous exchange takes place across the polyp's surface, nitrogenous waste is also excreted by diffusion. Most aquatic invertebrates excrete nitrogenous waste as ammonium (NH_4^+), which predominates over ammonia (NH_3) at seawater pH. Zooxanthellate invertebrates including corals, sea anemones and tridacnid clams may retain excretory ammonium or, in experimental incubations, even take up additional ammonium added to the seawater, provided there is enough light for symbiont photosynthesis. Such observations, going back to early work by Geddes (1882) and Pütter (1911), implied that the algal symbionts took up this excretory nitrogen and perhaps recycled it back to the animal host as amino acids. However, although starved zooxanthellate *Anemonia viridis* gained weight when supplied with ammonium-supplemented seawater (Roberts *et al*., 1999a) the exact role of zooxanthellae in allowing this symbiotic anemone to incorporate inorganic nitrogen into animal protein remains ambiguous (Roberts *et al*., 1999b).

Sea anemones osmoregulate in large part by adjusting their cellular free amino acid levels. Species found in stable salinities typically show high concentrations of taurine, a relatively inert amino acid that is unlikely to perturb enzyme function (a 'compatible solute') whereas species exposed to varying salinities rely on more labile amino acids such as glycine, alanine and glutamate that can be rapidly converted to osmotically inactive compounds if required (Shick, 1991). At the time of writing there have been no studies on the excretory physiology of the cold-water coral groups that are the focus of this book. Their occurrence in deep waters, removed from the fluctuating salinities of shallow seas, suggests cold-water corals will have little need to osmoregulate in response to salinity changes so we may speculate that their free amino acid compositions may mirror those of sea anemones from stable salinities showing significant levels of 'compatible solutes', notably taurine (e.g. Wang & Douglas, 1998; Roberts *et al*., 2001).

3.5.3 Nervous and endocrine control

Once again, very little is known about nervous or endocrine control in cold-water corals. Cnidarians are typically considered to have a nervous system based on a diffuse nerve net forming the simplest metazoan nervous system known, but recent work shows this view is an oversimplification, see below. Once again much of our understanding of cnidarian nervous control comes from work on sea anemones, which, despite the simplicity of their nervous system, show a great variety of behaviours from rapid contraction to locomotion and even the ability to climb onto gastropod shells occupied by hermit crabs as shown by *Calliactis parasitica* (Ross & Sutton, 1961). However, one study has examined nervous control and behaviour in a cold-water coral. Shelton (1980) reported observations on polyp behaviour and electrical conduction in *Lophelia pertusa*, using samples collected by bottom trawl from Rockall Bank in the northeast Atlantic. Electrical stimulation of the oral disc evoked a nervous or muscular response from the tentacles, showing that, like other anthozoans, *L. pertusa* possesses a nerve net. However, unlike most other colonial anthozoans, these electrical stimuli were not transmitted between polyps. As well as the nerve net, showing conduction velocities of $8-10\,\mathrm{cm\,s^{-1}}$, Shelton reported a slow conduction system ($4-5\,\mathrm{cm\,s^{-1}}$) that could be stimulated separately from the nerve net, but because this system was refractory and rapidly fatigued Shelton was not able to follow which behavioural processes it controlled. In anthozoans, the nerve net is typically responsible for transmitting signals from mechanical stimuli to evoke muscular contraction and tentacle or polyp retraction whereas the slow conducting systems are responsible for controlling the degree of polyp expansion.

Since Shelton's investigation in the late 1970s no studies have followed these preliminary observations of nervous control and behaviour in *L. pertusa*. It is worth repeating, as Shelton noted, that more studies of freshly collected material are needed to develop our understanding, particularly of the slow conduction system. The corals used by Shelton were collected by bottom trawl and did not ingest food, despite being fed in the laboratory for several months. Failure to feed over several weeks or months is a sign of stress or damage in *L. pertusa*, frequently noted from corals collected using bottom trawls. Improved access to remotely operated vehicles equipped with biological storage boxes to minimise collection stress and our improved understanding of cold-water coral food supply and nutrition make it possible to plan more comprehensive studies of their ecophysiology and neurobiology.

Recent work on cnidarian neurobiology is showing that the classic textbook view of nervous control mediated by a simple, diffuse nerve net may be an oversimplification. By using immunocytochemistry with neuron-specific antisera to visualise cnidarian nervous systems it now seems that members of this phylum have concentrations of neuronal elements in nerve rings and tracts often found with sensory structures in the oral disc region (Grimmelikhuijzen *et al.*, 2002). Cnidarians could even be considered to have rudimentary brains or central nervous systems (Anderson, 2004). Their nervous systems are also now known to use peptides as neurotransmitters. These neuropeptides are synthesised by similar enzyme pathways to those found in mammals implying that these features of animal nervous systems came about early and have been conserved during metazoan evolution (Grimmelikhuijzen *et al.*, 2002).

Thus there is some basis to our understanding of cnidarian nervous control. But what is known of hormonal or endocrine control? Indeed would simple animals made up from two cell layers without circulatory systems or organs be expected to possess endocrine control systems at all? Tarrant (2005) reviewed endocrine-like signalling in the Cnidaria and compiled a list of compounds found in cnidarians that are known to act as hormones in vertebrates. While a number of steroids, neuropeptides and other hormone-like compounds have been found, endocrine control has not been studied in the Cnidaria. Thus while considerable efforts have gone into understanding important aspects of tropical coral biology, such as the environmental cues for mass spawning, we do not know how the cues are translated by corals into physiological responses such as spawning or larval metamorphosis. However, examples of chemical communication and information on the possible roles of coral hormones both exist. Octocorals can synthesise a diverse array of diterpenes, prostaglandins and steroids (see Tarrant, 2005 for summary) some of which are toxic and deter predators while others have specific functions, such as a diterpene from *Lobophytum crassum* that acts as a sperm attractant (Coll *et al*., 1995). Interestingly, several studies have reported correlations between levels of steroid hormones and spawning in shallow-water scleractinian corals. Steroid sex hormones reached maximum levels just before spawning in *Montipora verrucosa* (Tarrant *et al*., 1999) and during spawning in *Euphyllia ancora* (Twan *et al*., 2003). On the other hand, levels of testosterone declined in both male and female *Sinularia polydactyla* (alcyonacean soft coral) after spawning (Slattery *et al*., 1999). This work raises the intriguing possibility that it may be feasible to identify the timing of cold-water coral spawning by measuring steroid levels in tissue samples taken throughout a seasonal cycle. It is to the evidence for mass spawning and the reproductive ecology of cold-water corals that we now turn.

3.6 Reproduction

As a group, corals show a variety of reproductive strategies; some species have separate sexes (gonochorism) while others are hermaphrodites. Corals also show variable modes of reproduction from species that spawn gametes into the water column to others that brood their larvae internally. At the time of writing, very little was known of the larval biology of any of the deep-water reef framework-forming cold-water corals. What information exists on the reproductive ecology of cold-water corals has only been gathered in recent years. Our understanding is based on examining gametogenic status from histological sections of preserved coral samples. These samples are either from corals found in historic deep-sea collections, or corals collected specifically for this analysis during recent research expeditions. Information on the complete gametogenic cycle is difficult to obtain since samples are generally not available during winter months, when weather conditions at high latitudes often prevent operations at sea. However, even given these constraints, some interesting trends in the reproductive ecology of deep-water scleractinians, Antarctic octocorals and North Pacific stylasterids are becoming apparent.

Whereas approximately three-quarters of shallow-water scleractinians are hermaphrodites (Fadlallah, 1983; Richmond & Hunter, 1990) most cold-water scleractinians examined so far are gonochoric. Of the 15 species reviewed by Waller (2005) just three species, *Caryophyllia cornuformis*, *C. ambrosia* and *C. seguenzae*, were hermaphroditic and these solitary corals all showed asynchronous, cyclical hermaphroditism. In other words any individual cup coral only showed viable sperm or eggs at any one time, a strategy that effectively prevents self-fertilisation. Unlike the *Caryophyllia* species, another solitary coral species, *Fungiacyathus marenzelleri*, was gonochoric, with corals from a 4100 m deep site in the northeast Pacific 50% less fecund than corals from a 2200 m deep site in the northeast Atlantic, perhaps because of food limitation at the deeper Pacific site (Waller *et al.*, 2002; Flint *et al.*, 2007).

Scleractinian corals do not have true gonads in the conventional metazoan sense (Fautin & Mariscal, 1991; Waller, 2005). Gametes are formed within the mesenteries with sperm developing in spermatocysts contained by a mesogleal envelope and eggs (oocytes) forming singly or grouped in small 'pockets' (Colour plate 12). Oocyte development in cold-water corals seems to mirror the pattern described by Fadlallah (1983) in shallow-water species. Oogonia attached to lamellae on the coral's mesenteries develop into pre-vitellogenic oocytes that migrate into the mesoglea. Here they develop a lipid-rich yolk to become vitellogenic (or yolk generating) oocytes. In the last stage of vitellogenesis before oocytes are released, a cortical layer forms around the oocyte.

One of the most spectacular displays from any marine ecosystem is synchronised coral spawning on shallow tropical reefs. Around 85% of shallow scleractinian species are broadcast spawners (Richmond, 1997) that show a variety of mass spawning dynamics, often closely related to the phase of the moon; for example in Guam spawning takes place 7–10 days after the July full moon (Richmond & Hunter, 1990). During mass spawning, gametes are released synchronously into the water column from several neighbouring colonies, thereby increasing the chances of cross-fertilisation. Several factors including temperature, light levels, tidal cycles and even chemical signals transmitted from released gametes are implicated in controlling the timing of spawning events (Richmond, 1997). At the great depths where cold-water scleractinians are found *in situ* coral spawning has not yet been directly observed but two lines of evidence suggest reef framework-forming cold-water corals broadcast spawn. Firstly, planula larvae have never been seen in histological sections of the reef framework-forming cold-water corals *Lophelia pertusa*, *Madrepora oculata*, *Solenosmilia variabilis*, *Goniocorella dumosa* or *Enallopsammia rostrata* (Burgess & Babcock, 2005; Waller & Tyler, 2005) and shallow corals from the same families (Oculinidae and Caryophylliidae) were all found to be broadcast spawners (Harrison & Wallace, 1990). The relatively shallow (3–100 m), facultatively zooxanthellate scleractinian *Oculina varicosa* is also a gonochoristic broadcast spawner that forms actively swimming planulae that settle after approximately three weeks (Brooke & Young, 2003), see discussion of larval biology in Section 3.7, p. 105.

But what might trigger spawning events allowing these corals to fertilise successfully? While the role of moonlight levels in controlling tropical coral spawning is now characterised to the extent that recent work is uncovering the genetic control of this circadian behaviour (Levy *et al*., 2007), the environmental triggers of cold-water coral spawning remain conjectural. Cyclical time signals could reach cold-water coral habitats in various ways. The seasonal cycles in food input reviewed earlier could provide an annual factor to synchronise reproduction in high-latitude reef framework-forming scleractinian corals (Burgess & Babcock, 2005; Waller & Tyler, 2005). This seasonal synchronisation fits with the reproductive pattern reported from invertebrates found shallower than 3000 m depth rather than that seen in truly 'deep-sea' species, which typically breed asynchronously, see review by Gooday (2002). Seasonally pulsed food input could promote various aspects of reproductive activity from initiating gamete development and promoting vitellogenesis to spawning and larval settlement (Tyler *et al*., 1982).

While food input is likely to be involved in controlling reproductive timing in areas with pronounced spring blooms, other factors may come into play in less seasonal areas and over shorter time periods to synchronise mass spawning. For example, while often found at considerable depths, cold-water coral habitats may still experience pronounced tidal cycles such as those reported in the northeast Atlantic by Roberts *et al*. (2005b) at the Sula Ridge reef complex (Norwegian margin, 280 m depth) and on the flanks of the Galway coral carbonate mound (Porcupine Seabight, 800 m depth). Tidal and annual temperature cycles in some areas, such as the gradual warming of the continental shelf noted around the Mingulay reef complex (Dodds *et al*., 2007), could all be implicated as potential environmental factors capable of triggering circadian behaviours in cold-water corals. For example, spawning in the Mediterranean gorgonians *Paramurica clavata* and *Eunicella singularis* coincides with warming spring seawater temperatures (Gori *et al*., 2007).

Most gorgonian corals are gonochoristic and, as with the Scleractinia, most studies of reproductive ecology have been based on shallow, warm-water species. However, efforts to understand the ecology of gorgonians that form important structural habitat in polar waters show that, despite the strong seasonal influences that characterise polar ecosystems, cold-water gorgonian reproduction may not differ radically from the reproductive patterns of octocorals at other latitudes (Orejas *et al*., 2007). For example, *Ainigmaptilon antarcticum* is an important component of the sessile invertebrate fauna of the Antarctic Weddell Sea (Colour plate 11). As seen in many other cold-water invertebrates, colonies of this primnoid coral from 150–600 m depth have slow gamete development with oocyte maturation times of more than a year (Orejas *et al*., 2002). Orejas *et al*. concluded that *A. antarcticum* most likely spawned large, yolk-rich oocytes in the late summer and autumn probably so the larvae could develop over winter ready to settle during the rich feeding conditions of spring and summer. A subsequent study of four other species highlighted the diversity of reproductive patterns in Antarctic gorgonians (Orejas *et al*., 2007). While all species were gonochoric, like most gorgonians, they showed different reproductive modes with three brooders (*Thouarella* sp., *Fannyella rossii*, *F. spinosa*) and one presumed to spawn (*Dasystenella acanthina*). Further differences were found in their reproductive cycles: the two *Fannyella* species showed just one size class of oocytes indicating annual periodicity whereas *Thouarella* sp. and *Dasystenella acanthina* both showed two oocyte size classes implying a reproductive cycle with overlapping generations, each longer than a year.

Recently, information on the reproductive biology of the stylasterid corals that form an important component of the spectacular so-called ‘coral garden’ habitats in the North Pacific (see Case study 5.2, p. 150) has been gathered. Brooke and Stone (2007) examined *Stylaster brochi*, *S. verrillii*, *S. campylecus*, *S. cancellatus*, *Errinopora nanneca*, *E. pourtalesi*, *Distichopora borealis*, *Cyclohelia lamellata*, *Crypthelia trophostega* along with two unidentified *Stylaster* and one unidentified *Distichopora* species. All 12 species were gonochoristic brooders and individual colonies contained gametes in various stages of development implying that these Alaskan stylasterid corals either reproduce continuously or have a protracted reproductive cycle. Unlike the scleractinian reef framework-forming species that probably broadcast spawn and seem to have highly dispersive larvae, the North Pacific stylasterids may mirror their shallow-water counterparts and produce short-lived planulae that settle close to parental colonies. If this is the case they will have limited dispersal capacities in all but the strongest water currents and recovery from any anthropogenic impact may be very slow (Brooke & Stone, 2007).

Assessing an organism’s ability to recover after impact requires an understanding of both reproductive and regeneration potential and, in the case of corals, this includes asexual propagation and fragmentation as well as their sexual reproductive potential or fecundity. The pioneering observations of Wilson (1979) were among the first to show that reef framework-forming scleractinians, like *Lophelia pertusa*, could continue to grow and divide after (bio)erosion of a parent colony begins to break it apart. Indeed molecular genetic evidence shows that some populations of *L. pertusa*, such as those on the Darwin Mounds in the northeast Atlantic, are composed of very few clones (Le Goff-Vitry *et al.*, 2004a), see Section 2.6, p. 61. But while asexual propagation and fragmentation seem integral to deep-water scleractinian reef and mound formation, there are no observations showing that stylasterid corals, such as those from the Aleutian Islands, continue to survive and grow after fragmentation (Brooke & Stone, 2007). Fecundity in corals is assessed by measuring oocyte size and number with the latter usually expressed as number of oocytes per polyp. Waller (2005) tabulates fecundity estimates from cold-water scleractinian corals ranging from 144 in *Enallopsammia rostrata* from the south Pacific to over 3000 oocytes per polyp in *Lophelia pertusa* from the northeast Atlantic. Typically there is an inverse relationship between fecundity and oocyte or polyp diameter (Burgess & Babcock, 2005) and we may expect significant advances in our understanding of cold-water coral reproductive periodicity, fecundity and spawning control as more seasonal and *in situ* studies are developed.

3.7 Larval biology and dispersal

As outlined, our understanding of reproductive ecology in cold-water corals is in its infancy and we know very little of larval biology and dispersal potential, although Brooke and Young (2005) have succeeded in following early larval development in *Oculina varicosa* (the facultatively zooxanthellate scleractinian that forms azooxanthellate banks at 70–100 m depth along the south-central region of Florida's Atlantic coast). The planula larvae from both brooding and spawning corals are ciliated, lipid rich and have chemoreceptors used in settlement, but brooded larvae are typically larger and can settle soon after release (Richmond, 1997). Given that the reef framework-forming cold-water corals all appear to broadcast spawn but their larvae have yet to be studied, it is interesting to speculate on their larval longevity, how far they could disperse and how long they could remain able to settle (larval competency). These issues are critical for designing ecologically meaningful marine protected areas to ensure long-term conservation (see Section 8.2.1, p. 255).

Lophelia pertusa rapidly colonises shipwrecks and oil platforms (Colour plate 13) suggesting it has a larval phase capable of spreading coral colonies rapidly to new substrata, provided other conditions such as temperature and food supply discussed earlier are suitable. Roberts (2002) used evidence of *L. pertusa* colonisation of oil platforms in the North Sea to speculate that these recruits came from the inflows of Atlantic water to the North Sea. Furthermore, if coral planulae in cold Atlantic waters remained competent for approximately twice as long as planulae from tropical corals, then they may be capable of dispersal times of up to 100 days. There is an almost exponentially negative relationship between

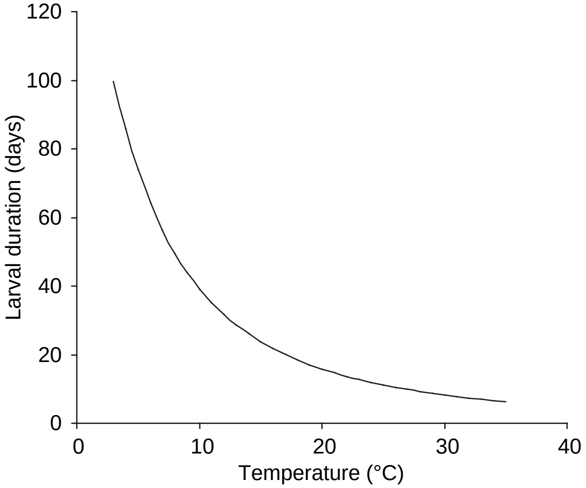


Fig. 3.13. Graph of the relationship between water temperature and planktonic larval duration. Curve represents population-averaged relationship described by O'Connor *et al.* (2007):

$$\ln(\text{larval duration}) = 3.17 - 1.34 \times \ln(T/\mathrm{T_c}) - 0.28 \times (\ln(T/\mathrm{T_c}))^2$$

where T = temperature and $\mathrm{T_c} = 15°\mathrm{C}$. This model was derived from published experimental studies from six phyla comprising six fish and 66 invertebrate species. Figure redrawn from O'Connor *et al.* (2007), with permission of the National Academy of Sciences of the USA.

length of larval duration and water temperature (Fig. 3.13) that has recently been compared, and found to be quantitatively constant, across a range of marine animals (O'Connor *et al.*, 2007). Although no cnidarian species were used in this meta-analysis, O'Connor *et al.*'s modelled relationship between water temperature and larval duration gives larval durations of 64 days for larvae at 6°C and 35 days at 11°C. Interestingly, the modelled value of 11 days larval duration at 25°C compares well with the 14–23 days it took larvae of *Oculina varicosa* to show signs of settling behaviour in laboratory studies at this temperature (Brooke & Young, 2005).

Oculina varicosa occurs at depths up to 100 m off south-central Florida where it experiences a wide temperature range from almost 30°C to less than 10°C associated with periodic upwelling of colder, nutrient-rich water along the Florida Shelf. Given this temperature range, and the facultative zooxanthellae symbiosis, *O. varicosa* can be considered in many senses a transitional ecology between the cold-water reef framework-forming scleractinians and the shallow-water tropical reef corals. At the time of writing, it is the only deeper-dwelling habitat-forming scleractinian for which spawning and larval behaviour have been studied. The first observations of *O. varicosa* spawning were made from coral samples that spawned shortly after collection at sea (Brooke & Young, 2003). Subsequent

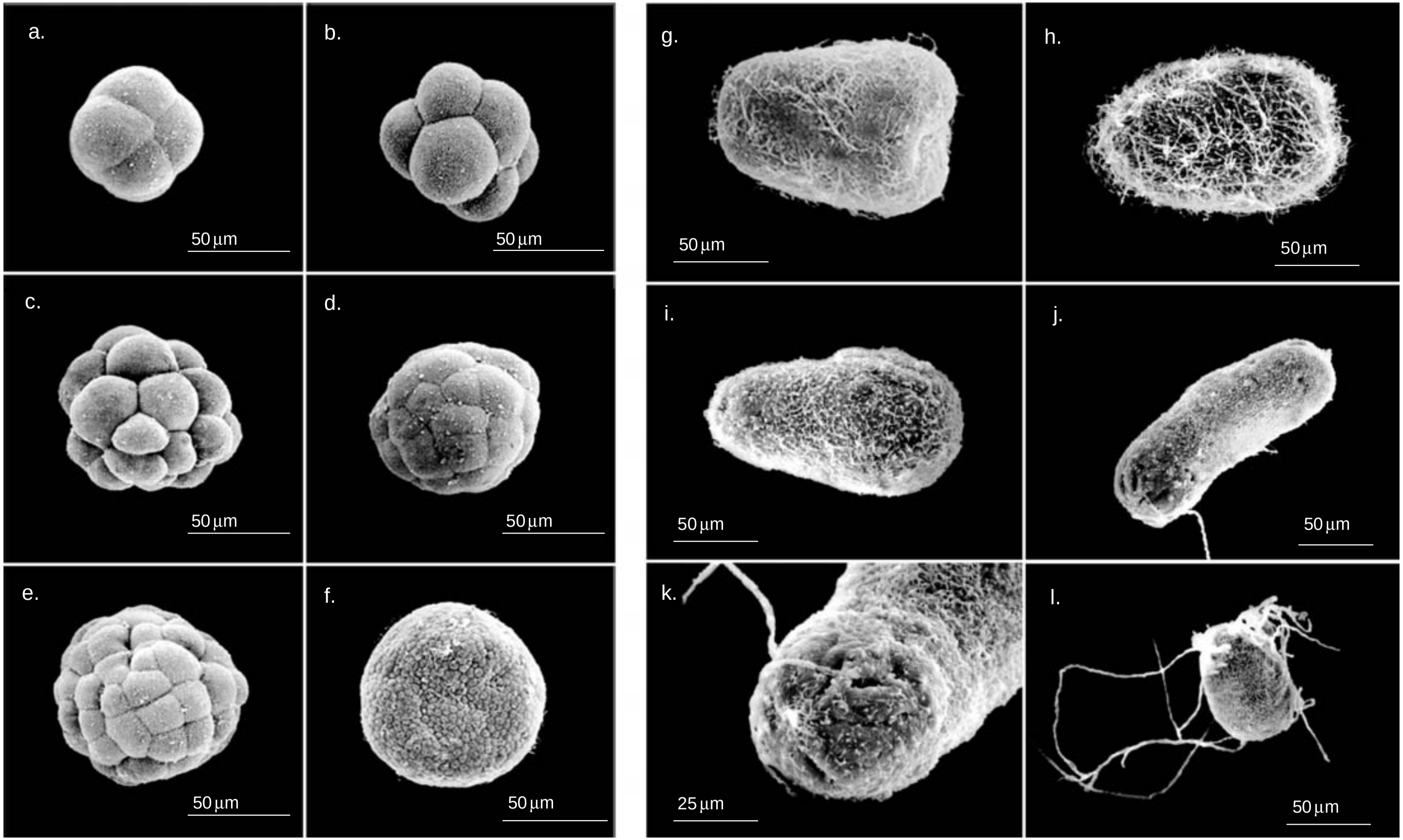


Fig. 3.14. Embryonic and larval development of the facultatively zooxanthellate scleractinian *Oculina varicosa* at 25°C. Scanning electron micrographs of embryonic stages: (a) 4-cell, (b) 8-cell, (c) morula, (d) early blastula, (e) late blastula, (f) late gastrula. Micrographs of larval stages: (g) 24 hours post-ciliation, (h) 7 days, (i) 14 days, (j) 21 days, (k) detail of nematocyst on larva at 21 days, (l) numerous nematocysts released by larva aged 10 days. Figure redrawn from Brooke and Young (2005), with permission of Springer.

laboratory study followed embryonic and larval development (Fig. 3.14) through to early indications of settlement behaviour when larvae became negatively phototactic (Brooke & Young, 2005).

Thus since the year 2000 our understanding of cold-water coral reproduction has improved immeasurably. However, there remains a long way to go before it can be said that we have unravelled reproductive periodicity, spawning cues and the circadian systems that may operate to control the timing of reproduction. While we have insights into the larval biology of shallow-water reef corals and *Oculina varicosa*, larvae from other cold-water reef framework-formers have yet to be sampled and studied. However, evidence from their rapid colonisation of man-made structures implies these species have effectively dispersing planulae that once settled form discrete coral colonies. It is to the structures formed by these coral colonies and the habitats they develop that we now turn.

4

Reefs and mounds

> *Even some zoologists and geologists perennially express surprise not only that corals exist in deep cold waters, but that in certain instances they create appreciable deposits of calcium carbonate, in the form of accumulations of their skeletal remains.*
>
> Coral banks occurring in deep water on the Blake Plateau
> Thomas R. Stetson, Donald F. Squires and Richard M. Pratt (1962)

Cold-water coral reefs and coral carbonate mounds are morphological features formed through complex interactions between biological and geological processes under suitable hydrodynamic conditions. Such interactions are common in marine systems with biological activity having a profound effect on a number of sedimentological processes: from diatom stabilisation of mudflat surfaces, to the role of algae in carbonate grapestone formation and the development of deep-water bioherms. Marine organisms can strongly influence their sedimentary environments and where their activities are focused in one place, distinct biogeological structures may be formed. Such scenarios often involve enhanced sediment accumulation through substratum stabilisation and/or sediment trapping and usually benefit the organisms in question, for instance by giving them a preferential position from which to feed and isolating them from the effects of scouring bedload transport.

Such biogeological formations are not only common in the geological record, because they form persistent features, but also because such positive interactions are ubiquitous throughout Earth history. In fact stromatolites, which form some of our first widespread evidence for life and date from 3.5 billion years ago in the Precambrian (Walter, 1983), resulted from such interactions, notably sediment cementation by cyanobacterial biofilms (Allwood *et al.*, 2006; Lepot *et al.*, 2008). On a much larger scale, reef framework-forming organisms have produced large-scale biogeological structures throughout the geological record (Monty *et al.*, 1995) with examples such as the Upper Ordovician carbonate mounds of

Alabama, USA (Read, 1982), Devonian Canning Basin sponge reef complex, northwestern Australia (Webb, 1996; Wood, 1999, 2000), Lower Carboniferous (Visean) Cracoean reefs, northern England (Mundy, 1994), Carboniferous Waulsortian mud mounds, Ireland and Belgium (Lees & Miller, 1995; Webb, 2002) and the Permian Capitan reef of Texas and New Mexico, USA (Wood *et al*., 1996; Kirkland *et al*., 1998).

4.1 Reef initiation and development

We outline the use of the term 'reef' with respect to cold-water corals in Topic box 2.1, p. 23 and discuss the term 'coral carbonate mound' in Section 4.3 below. A potential cold-water coral reef or mound begins with the settlement of individual coral larvae that grow to form coral colonies fixed on suitable hard substrata. If environmental conditions are favourable, then new coral larvae will continue to settle and the colonies will continue to grow in stature. As they grow coral colonies will intermingle and eventually their increased density will lead to the development of coral 'thickets' (Squires, 1964). The coral thicket provides support and protection for other organisms that become attracted to the new habitat. Differentiation between live and dead coral framework increases over time, resulting in distinct faunal zonation patterns of species richness and composition. Species attracted to the coral thickets also contribute to reef sediments and may play important roles in continued reef development. This is explored in more detail in the next two chapters although it is worth highlighting here the important role of bioeroders and reef-aggregators.

Bioeroders, principally sponges and fungi, topple coral colonies by attacking the dead, exposed skeleton at their bases, even though the coral may still be live and growing at the top. Bioerosion is a key process forming coral rubble. This rubble may then provide a substratum for renewed coral settlement, be incorporated into the reef sediment to form packstones or be further bioeroded to produce micritic components of reef sediment (see Topic box 4.1). Other organisms may even actively promote reef aggregation. The symbiotic polychaete worm *Eunice norvegica* not only stimulates excessive coral calcification strengthening the framework, but can also move small colonies and rubble together to improve its microhabitat and perhaps accelerate reef patch development (Roberts, 2005). With the development of skeletal debris providing substrata for renewed coral growth, the coral thickets now move into the coral 'coppice' phase of development (Squires, 1964) and from there eventually to form reefs. The process outlined above can be described in geological terms as

Topic box 4.1 **What is a limestone?**

Cold-water coral reefs and mounds are composed of limestones, calcareous muds and sands, and non-calcareous muds and sands. They may or may not be lithified. Muds and sands are classified as calcareous if they contain more than 10% calcium carbonate and limestones if they contain more than 50% calcium carbonate.

Calcareous components of reef/mound sediments include micrite, biological remains (including calcareous ooze) and precipitated calcium carbonate. Micrite is composed of calcite or aragonite crystals <4 μm long often formed by (bio)erosion. Calcareous ooze is composed mainly of microscopic biological remains (calcareous plankton) such as foraminiferans, coccolithophores and pteropods.

Limestones are commonly classified using the Dunham (1962) scheme including the modification for reef rocks by Embry and Klovan (1972). The scheme is based on limestone composition and structure and is outlined in Fig. 4.1 below.

<table>
<tr><td colspan="6">ALLOCHTHONOUS LIMESTONE
Original components not organically bound during deposition</td><td colspan="3">AUTOCHTHONOUS LIMESTONE
Original components organically bound during deposition</td></tr>
<tr><td colspan="4">Less than 10% >2 mm components</td><td colspan="2">Greater than 10% >2 mm components</td><td rowspan="4">By organisms that build a rigid framework</td><td rowspan="4">By organisms that encrust and bind</td><td rowspan="4">By organisms that act as baffles</td></tr>
<tr><td colspan="3">Contains lime mud (<0.03 mm)</td><td>No lime mud</td><td rowspan="4">Matrix-supported</td><td rowspan="4">>2 mm component-supported</td></tr>
<tr><td colspan="2">Mud-supported</td><td colspan="2" rowspan="3">Grain-supported</td></tr>
<tr><td rowspan="2">Less than 10% grains (>0.03 mm–<2 mm)</td><td rowspan="2">Greater than 10% grains</td></tr>
<tr><td colspan="3">BOUNDSTONE</td></tr>
<tr><td>MUD-STONE</td><td>WACKE-STONE</td><td>PACK-STONE</td><td>GRAIN-STONE</td><td>FLOAT-STONE</td><td>RUD-STONE</td><td>FRAME-STONE</td><td>BIND-STONE</td><td>BAFFLE-STONE</td></tr>
</table>

Fig. 4.1. The Dunham classification for limestones based on depositional texture. Reproduced from Embry and Klovan (1972) with permission of Springer.

the progress from biocoenosis to thanatocoenosis to taphocoenosis and is drawn schematically in Fig. 4.2.

Wilson (1979) noted that under certain situations, the growth of living corals on dead and bioeroding coral skeleton will develop circular structures, the so-called 'Wilson rings', consisting of a ring of live coral surrounding a core of dead coral as the colonies grow outwards from the centre. As these colonies age, autochthonous skeletal debris from the corals and associated shelly fauna adds to the reef sediment. This is the point where the proportion of living versus dead corals shifts to the latter. In the final stage, the reef is characterised by a relatively thin outer rim of living corals. In a typical cold-water coral reef, the volume of exposed dead coral framework by far exceeds the volume of living coral. A current-driven faunal zonation will become

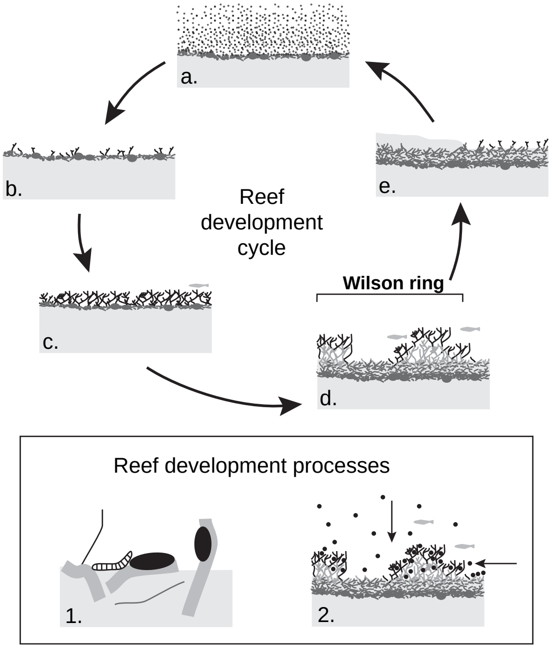


Fig. 4.2. Reef development cycle and processes. (a) Coral larvae settle on suitable hard substrata and (b) start to form small isolated or grouped colonies. (c) Continued coral colony growth leads to intermingling of coral colonies and the development of coral thickets with associated fauna forming a distinct biocoenosis. (d) The thicket reaches the coppice stage, possibly with Wilson rings, and a well-developed biocoenosis with a thanatocoenosis of dead coral frameworks and rubble beneath. (e) If environmental conditions change then the corals may die and the reef is bioeroded to coral rubble. This may become covered by sediment or form a site for new coral larvae to settle (a). The closure of this cycle now sets the stage for coral carbonate mound development. During reef development stages (c) to (e), key biotic and sedimentary processes have a major control on reef development. At the base of the reef (1) bioeroders topple dead coral colonies contributing to coral rubble where it may be further bioeroded to make micrite or recolonised by more coral recruits (possibly aided by the coral-aggregating behaviour of *Eunice norvegica*) or incorporated into the sediment as bioclasts (taphocoenosis). (2) Coral colonies also baffle hemipelagic and bedload sediment which is volumetrically important and may also help structurally support coral colonies.

established as current-exposed areas generally harbour a distinct community, different from that in sheltered areas (Mullins *et al*., 1981; Messing *et al*., 1990).

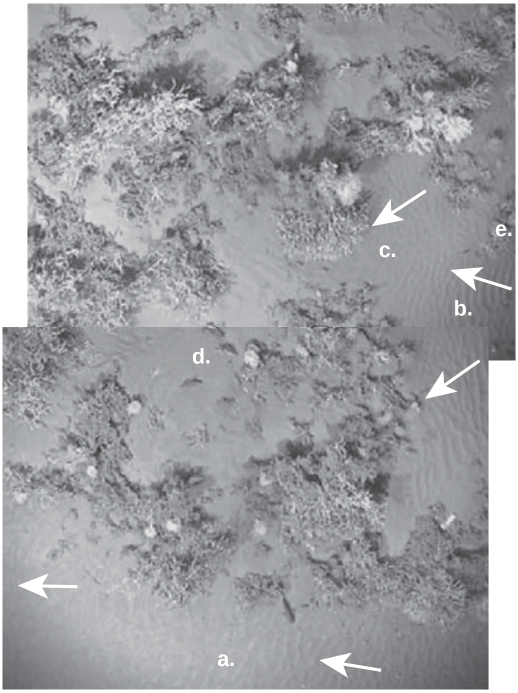


Fig. 4.3. The interaction of bedload sand transport (direction indicated by arrows) and coral colonies from the edge of a cold-water coral thicket (Moira Mound, Porcupine Seabight, northeast Atlantic). (a) Sand ripples with bifurcated crests beyond the coral thicket turn into (b) straight-crested ripples at the edge of the coral thicket as currents slow down due to thicket-induced frictional drag. By (c) even slower current speeds produce smaller bedforms and a transition to planar beds as currents diminish within the coral thicket where (d) they become too slow to form mobile bedforms generating a zone of sediment accumulation. At (e) altered ripple crest alignment and downstream size show how a coral colony retards current flows in its vicinity. Seabed image courtesy of the Alfred-Wegener-Institut für Polar- und Meeresforschung and the Institut Français de Recherche pour l'Exploitation de la Mer.

4.2 Reef sedimentation

As well as bioclastic material, another equally important component of reef sediment is hemipelagic material trapped within the reef framework as it grows. Coral colonies increase seabed surface roughness, retard water flow in the benthic boundary layer and increase turbulence and small-scale eddies as the flow passes around and through individual colonies (Mullins *et al.*, 1981), see Fig. 4.3. Other organisms that grow into the water column, including sea grasses (Scoffin, 1970) and bryozoans (Anderskouv *et al.*, 2007), can cause similar sediment-trapping processes. Coral–hydrodynamic interactions have three major effects. (1)

Decreased flow within coral frameworks causes bedload-transported sediment to deposit around the coral colonies (Fig. 4.3a–d). Typically, on-mound grain sizes are finer than those off-mound (Dorschel *et al.*, 2007a). (2) Current flow tends to become deflected around coral colonies, modifying bedload sediment transport directions into the reef and retaining sediment between and around coral colonies (Fig. 4.3e). (3) Further up the reef or mound beyond the reach of bedload transport process, deposition of suspended sediment may also be enhanced because slower currents have reduced sediment-carrying capacity. This implies that different sedimentological processes may affect reef edges (bedload and suspended sediment) and reef crests (suspended sediment only).

The resulting localised increase in sediment accumulation is known as sediment trapping or baffling (see Flügel, 2004). The detrital particles themselves generally do not sink as individual grains. Instead, they tend to generate planktonic aggregates known as 'marine snow', a major element of the pelagic–benthic transfer of nutrients and sediments, see Section 3.3.3, p. 81 (Kiørboe, 2001; Kiriakoulakis *et al.*, 2007). The physical trapping effect may be increased by active biological capture of sediment particles through suspension-feeding by the framework-forming corals themselves and other reef organisms such as zoanthids, alcyonarians, gorgonians and crinoids, which tend to colonise preferentially on up-current slopes of reefs (Messing *et al.*, 1990; Mienis *et al.*, 2006; De Mol *et al.*, 2007; Wienberg *et al.*, 2008).

Sediment baffling is a major process in reef development and is the most important factor in creating three-dimensional relief. It also brings about deposition at the reef site in an otherwise non-depositional regional environment. For example, Wheeler *et al.* (2008) noted a positive relationship between Darwin Mound relief and current intensity reflecting increased sediment flux. This has important implications for coral carbonate mounds as palaeoenvironmental recorders. Finally, the accumulation of sediment around coral frameworks may also provide structural support, even preventing bioeroded coral colonies from toppling (Wheeler *et al.*, 2007).

4.2.1 Matrix sediment and deposits

Investigations of cold-water coral reef sediments taken both from beneath living frameworks and from ancient counterparts display two sedimentary origins: autochthonous and inherited (Squires, 1964; De Mol *et al.*, 2002; Freiwald *et al.*, 2002; Rüggeberg *et al.*, 2005). Autochthonous sediment, including diagenetic cements, are considered in Section 4.4.5 below. Biodetrial-inherited sediment components are always derived from fragmented or (bio)eroded corals (including stylasterids and the internodes of isidid octocorals) and various proportions of the

Table 4.1 *Structural categories of organic reefs and carbonate mud mounds (from Riding, 2002, Table 1). Asterisks denote those applicable to cold-water coral reefs. Note that skeletal material makes up a small proportion, if any, of carbonate mud mounds. This is not typical of coral carbonate mounds sampled to date. Reproduced with permission of Elsevier.*

- ORGANIC REEFS*
  - **Matrix-supported reefs***
    - Agglutinated microbial reefs (in place skeletons few/absent)
    - Cluster reefs* (in place skeletons close but not in contact)
      - Close cluster reefs*
      - Spaced cluster reefs*
    - Segment reefs* (skeletons disarticulated)
  - **Skeleton-supported reefs***
    - Frame reefs* (in place skeletons in contact)
      - Open frame reefs*
      - Filled frame reefs*
  - **Cement-supported reefs***
    - Cement reefs*
      - Non-skeletal cement reefs: tufa and travertine cement reefs
      - Skeleton-cement reefs*
- CARBONATE MUD MOUNDS
  - **Carbonate mud mounds** (organic/inorganic, in place skeletons few/absent)
    - Low-relief mud mounds
    - High-relief mud mounds

Fig. 4.4. A computed tomography (CT) scan of a core from a filled frame reef (*sensu* Riding, 2002) from Trænadeep, northern Norwegian Shelf. Image courtesy of Siemens AG, Healthcare Sector.

associated fauna such as molluscs, serpulids, brachiopods, bryozoans, barnacles, echinoderms, ostracods and benthic foraminiferans (De Mol *et al*., 2002). The inherited sediment material is volumetrically more important and consists of fine-grained detritus from clay and silt, to fine sand-sized classes of biogenic (planktonic foraminiferans, coccolithophorids, pteropods) or siliciclastic origin. This imported material creates a muddy matrix, often referred to as biogenic ooze, in which the coarser skeletal components are embedded. In other words, reef and mound sediments generally have a distinctly bimodal grain size spectrum.

4.2.2 Deposit-based cold-water coral reef classification

Coral carbonate mounds form through periods of successive reef development with each reef forming under the environmental conditions that existed at the time. Correspondingly, the reef deposits contained in coral carbonate mounds may have different architectures depending on the balance of formation processes: the biotic versus abiotic sediment contributions, extent of bioerosion and cementation. The classification of reef deposits and reef forms is dealt with extensively in the organic reefs and carbonate mud mounds review by Riding (2002), see also Monty *et al*. (1995). Riding provides a structural classification of organic reefs and carbonate mud mounds, based on biological–lithological component ratios, biological growth architecture and relief (Table 4.1). Some of these terms are applicable to cold-water coral reefs, namely cluster reefs (close and spaced), segment reefs, frame reefs (open and filled) and skeleton-cement reefs. Figure 4.4 shows a computed tomography (CT) scan through a core from a cold-water coral reef. The CT scan clearly shows the three-dimensional structure of the coral architecture with interstitial sediment infill appearing transparent in this image. Using Riding's (2002) classification, the core comes from a filled frame reef. Riding (2002) also illustrates schematically how the descriptive classification scheme relates the main processes of reef development (sediment trapping, skeleton formation and/or cementation) to the main mode of sediment support (matrix supported, skeleton support or cemented). A version of Riding's schematic modified for cold-water coral reefs is given in Fig. 4.5.

4.3 Defining coral carbonate mounds

In this book we distinguish between cold-water coral reefs and coral carbonate mounds. In Chapter 2 we introduced the concept of cold-water corals as reef framework-forming organisms. We define these structures as biogenic reefs on the basis that they are long-lived, their growth is balanced by (bio)erosion, they

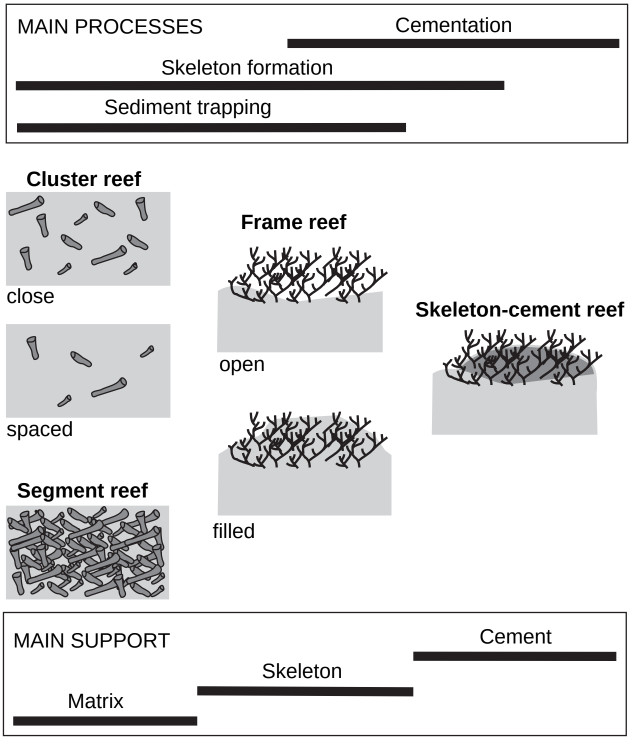


Fig. 4.5. A structural classification for cold-water reefs based on an adaptation of Riding's (2002, Fig. 37) schematic. Figure adapted from Riding (2002) with permission of Elsevier.

form local topographic highs that alter hydrodynamic and sedimentary regimes, and they form structural habitats for many other species (see Topic box 2.1, p. 23). Over time, reefs may die due to changes in environmental conditions. Their fossils remain and accumulate interstitial sediments, which may persist and form elevated structures on the seafloor. These may become preferential sites for renewed reef formation, possibly thousands or tens of thousands of years later (see Section 4.4 below). Following terminology used in Roberts *et al.* (2006), we define coral carbonate mounds as topographic seafloor structures that have accumulated through successive periods of reef development, sedimentation and (bio)erosion. They may or may not support contemporary reefs and typically contain stratified sequences of reef deposits separated by non-reef (typical seafloor) sedimentary units and erosion surfaces. Carbonate content may or may not be compositionally dominant. We discuss the appropriateness of this terminology below.

Coral carbonate mounds formed by the interaction of cold-water coral growth and sedimentary processes come in a variety of shapes and sizes. Furthermore, the internal composition of such mounds may vary from region to region depending on the dominance of biological versus geological mound-building processes and the properties of background sediment input. The composition of the mound deposits also varies over time, and hence stratigraphically with depth within the mounds, due to variation in mound development processes and palaeoenvironmental conditions. The heterogeneity of coral carbonate mounds therefore makes a strict, narrow definition based on physical properties problematic. Nevertheless, all mounds have one key aspect in common: they owe their origin and development to the reef framework-forming potential of cold-water corals.

Given the degree of variation in mound attributes it is perhaps not surprising that a bewildering array of terms has been coined to define coral carbonate mounds (Table 4.2). Many of these terms were appropriate for the specific mounds under consideration but some have then been erroneously applied to other mounds whose features differ or are unsubstantiated. Coral carbonate mounds were often initially referred to as 'coral banks'. The term 'bank' originally referred to any positive topographic seafloor feature including relatively small offshore sandbanks and rock outcrops as well as extremely large, submerged, rifted continental blocks. It also encompassed both cold-water coral reefs and mounds, leading to the confusing situation that banks (coral) often occur on banks (other larger-scale topographic features).

To avoid this confusion, and more importantly to distinguish 'single generation' reefs from mounds formed by successive periods of reef development, the term 'carbonate mound' has become popular, often with the use of qualifying adjectives (e.g. giant, cold-water coral, deep-water, etc.). However, the term carbonate mound has connotations because it has been used to describe a number of carbonate-dominated mound features formed by a variety of organisms throughout the geological record (e.g. bryozoan mounds and algal-bacterially mediated mud mounds). This term appeared in the geological literature to make a clear distinction between the large number of Mesozoic biogeological structures formed by corals (carbonate reef deposits) and those formed by different organisms and processes common in both the Palaeozoic and Mesozoic (carbonate mounds). The adoption of the term carbonate mounds to describe Cenozoic cold-water coral biogeological structures is therefore perhaps a little odd. Early studies were mainly based on seismic imaging and lacked access to drilled cores so the terminology arose based on speculation about internal structures and growth processes. Given what we now know from rare terrestrial outcrops (see Section 6.2, p. 180) and drilled cores, it is probably more appropriate to consider these structures as composite reefs. However, such a shift in terminology, however appropriate, is probably too radical to become adopted generally. Another important consideration is that a true carbonate mound contains predominately carbonate sediment. But sediments from

Table 4.2 *Examples of coral carbonate mound terminology as applied in the literature showing the dominant use of the term 'carbonate mound'.*

Term	*Reference*
Bioherm	Mullins *et al.* (1981); Mortensen *et al.* (1995); Henriet *et al.* (1998)
Carbonate knolls	Hovland *et al.* (1994a)
Carbonate mound (inc. qualifying adjectives: coral, giant, deep-water, deep-sea, cold-water coral or cold-water coral covered)	Henriet *et al.* (2001); Akhmetzhanov *et al.* (2003); Bailey *et al.* (2003); Beyer *et al.* (2003); O'Reilly *et al.* (2003); van Weering *et al.* (2003); Dorschel *et al.* (2005); Frank *et al.* (2005); Roberts *et al.* (2005b); Rüggeberg *et al.* (2005); Wheeler *et al.* (2005c); Mienis *et al.* (2006); Roberts *et al.* (2006); Dorschel *et al.* (2007b); Mienis *et al.* (2007); Rüggeberg *et al.* (2007); Wienberg *et al.* (2008)
Cold-water coral mounds inc. deep-water coral mounds	O'Reilly *et al.* (2004); Wheeler *et al.* (2005a); Williams *et al.* (2006b); Henry & Roberts (2007); Kano *et al.* (2007); Wheeler *et al.* (2007)
Coral bank	Dons (1944); Le Danois (1948); Teichert (1958); Stetson *et al.* (1962); Squires (1964); Cairns & Stanley (1982); Hovland *et al.* (1998); De Mol *et al.* (2002); Huvenne *et al.* (2003); De Mol *et al.* (2005); Huvenne *et al.* (2005); De Mol *et al.* (2007)
Coral-topped mound	Masson *et al.* (2003)
Deep-water coral reef mound	Freiwald *et al.* (1997a)
Giant carbonate mud mound	Kenyon *et al.* (2003)
Lithoherm	Neumann *et al.* (1977); Messing *et al.* (1990); Paull (2000); Wenner & Barans (2001); Reed *et al.* (2006)

some total coral carbonate mound sequences are dominated by siliceous lithics. In most cases where the term carbonate mound has been applied, the compositional dominance of carbonates in mound sequences has not been verified.

We must therefore be very clear that in using the popular terminology of coral carbonate mound we cannot assume that the mound is necessarily dominated by carbonate, although coral carbonate is a compositionally important and diagnostic component. We recognise that the term coral carbonate mound has become widely accepted in the scientific literature and is now being used by government

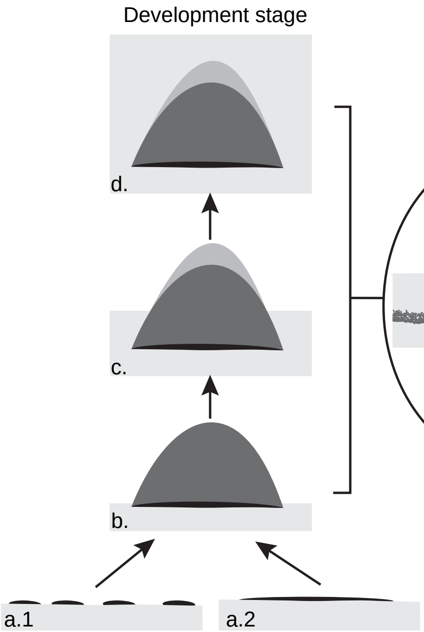


Fig. 4.6. Coral carbonate mound development model showing phases of mound development through cyclical periods of reef growth. Coral carbonate mounds may start from (a.1) many small reefs that merge or (a.2) from an extensive lateral reef. (b) Once established the mound grows quickly under optimal hydrographic conditions trapping both bedload and hemipelagic sediment. (c) Mound growth then slows and becomes more susceptible to erosion as it grows out of its optimal water mass and is starved of bedload sediment. (d) Eventually off-mound sedimentation rates may overtake mound growth rates and it becomes buried. Details of reef development cycle are given in Fig. 4.2.

agencies and conservation organisations. We therefore adopt the term here in line with popular convention to aid comprehension.

4.4 Mound development

A number of processes acting on a range of temporal and spatial scales need to be considered when formulating a model to explain the development of coral carbonate mounds. There are several such development models, including those by De Mol *et al.* (2002, 2005), Henriet *et al.* (2003), Kenyon *et al.* (2003), Dorschel *et al.* (2005), Huvenne *et al.* (2005), Kozachenko (2005), Roberts *et al.* (2006) and Rüggeberg *et al.* (2007). These models suggest biological reef growth cycles operating on decadal to millennial timescales and longer geological mound growth phases operating on millennial to million year timescales. The conceptual model presented here (Fig. 4.6) is a synthesis of these existing models and suggests an initiation phase of coral thickets or small-scale ‘incipient’ mounds, such as the Moira and Darwin Mounds in the northeast Atlantic. This is followed by rapid vertical mound growth with cyclical reef development providing the process to build larger mounds. In this section we consider these processes and attempt to develop a consistent interpretation of the inception of coral carbonate mounds and their development from an early mound growth phase through to eventual mound burial.

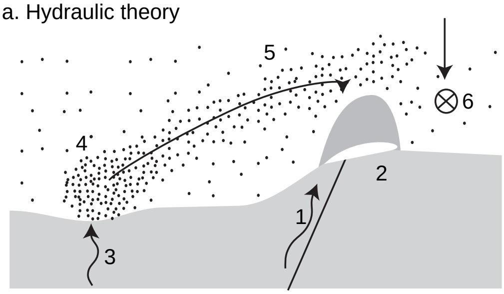
4.4.1 Mound initiation

The topic of coral carbonate mounds has until recently been dominated by discussions on the mechanisms of mound initiation and growth. These have focused on the merits of the hydraulic theory, with initiation and growth stimulated by hydrocarbon seeps, versus growth and initiation mechanisms governed by environmental conditions optimal for coral growth with entrapped sediment allowing vertical mound growth over time (Fig. 4.7). The details and merits of these theories are discussed in Section 3.3, p. 73 and are not repeated here. However, at present there is a lack of direct evidence for the influence of hydrocarbon seeps on mounds and/or coral growth in contemporary settings (e.g. Paull *et al.*, 2000; Masson *et al.*, 2003; Mienis *et al.*, 2007).

Proponents of the hydraulic theory suggested that cold-seeps may still play a key role in mound initiation and may explain the spatial distribution patterns of coral carbonate mounds. There are several lines of evidence to suggest support for this idea. (1) Coral carbonate mound provinces (discrete regional areas with a high density of coral carbonate mounds) tend to be located over hydrocarbon reservoirs and have similar spatial dimensions to those reservoirs. (2) Many coral carbonate mounds occur over, or are aligned with, faults that might be hydrocarbon seepage pathways. Examples include the Hovland Mounds (Hovland *et al.*, 1994a) and the Pelagia Mounds (Wheeler *et al.*, 2005a). (3) At least one hydrocarbon fluid migration model (Naeth *et al.*, 2005, 2007) predicted seepage near coral carbonate mounds (in the Belgica mound province, Porcupine Seabight, northeast Atlantic).

However, several counter-arguments can also be made. (1) Coral carbonate mound provinces are not exclusively found above hydrocarbon reservoirs. In fact where this appears to be the case it may be a coincidence because the areas of continental margin where mound formation is favoured by local hydrographic factors are similar in scale to the underlying hydrocarbon reservoirs. (2) Close examination of the correlations between mounds and underlying fault systems suggests that these are not strong enough and many features interpreted as faults are seismic artefacts (Bailey *et al.*, 2003). When present it is possible that faults play a different role generating elevated seabed topography that favours reef or

a. Hydraulic theory



b. Environmental control theory

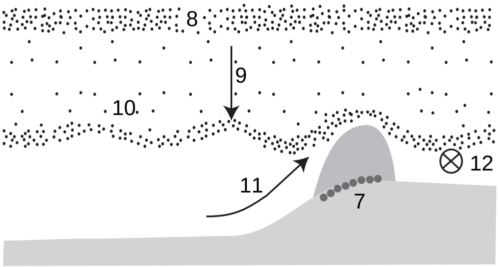


Fig. 4.7. Schematic diagram summarising the hydraulic and environmental control theories for mound initiation and development. (a) Hydraulic theory. (1) Gas seepage may lead to the development of (2) methane-derived authigenic carbonates that may act as a substratum for coral settlement. (3) Gas seepage at the seabed may provide a source of food increasing (4) biomass along the food chain. (5) Cold-water corals are supported by this food chain. (6) Along-slope and hemipelagic sedimentation provides a lithic sediment infill to the reef structure. (b) Environmental control theory. (7) Erosion of the seabed by strong currents may generate suitable coarse-grained substrata for coral settlement. (8) Surface primary productivity underpins the food chain. (9) This settles through the water column as marine snow and may (10) become concentrated at water mass boundaries and transported to the coral reef possibly assisted by internal waves. (11) Benthic hydrodynamics help to enhance food flux and prevent coral polyp smothering by fine sediment deposition. (12) Along-slope and hemipelagic sedimentation provides a lithic sediment infill to the reef structure.

mound formation. (3) Isotopic analyses of coral skeletons and tissue suggest that they metabolise contemporary carbon derived from surface ocean productivity and are not reliant upon, and do not recycle, ancient carbon from hydrocarbon seeps. (4) Recently, samples from the base of a coral carbonate mound revealed no evidence for the role of enhanced hydrocarbon concentrations in either mound initiation or development (Williams *et al.*, 2006b), see Case study 4.1, below. The now widely, but not universally, accepted theory of mound initiation is that coral carbonate mounds form in the same way as any other cold-water coral reef.

Case Study 4.1 **Challenger Mound, northeast Atlantic**

Despite many years of research, the complete story of coral carbonate mound initiation and development remained speculative due to a lack of data. Mound size (>100 m height) and location (600–800 m water depth) required seabed drilling to obtain the necessary sample material. Previous piston and gravity coring could only sample the upper sequences recording Late Pleistocene mound growth in the latter stages of mound development (see Section 1.2.3, p. 15).

In May 2005 it became practical to reach further back into the mound's history through Integrated Ocean Drilling Program (IODP) Expedition 307, which drilled five complete records through the Challenger Mound and into underlying strata as well as flank boreholes and upslope off-mound boreholes in the Belgica mound province (Porcupine Seabight, northeast Atlantic, see Fig. 4.8). The Challenger Mound is one of 66 mounds in the Belgica mound province (De Mol *et al.*, 2002; Van Rooij *et al.*, 2003) elevated nearly 150 m above the seabed with its summit at around 800 m water depth. It is not currently covered by a living coral reef but coral rubble. Five sites were drilled near the mound summit (U1317) recovering a 155 m sedimentary record through the mound consisting of unlithified floatstones, rudstones and wackestones (see Topic box 4.1, p. 110). The recovered sediments contained *Lophelia pertusa* with smaller quantities of *Madrepora oculata* throughout the mound, including the mound base, and consisted of alternating coral and sediment-dominated units. Lithic components were mainly fine silts and clays with some sands near the base. The presence of coral throughout the mound sequence made it possible for the first time to state definitively that cold-water corals played a key role in the initiation and development of coral carbonate mounds (Williams *et al.*, 2006b; Kano *et al.*, 2007).

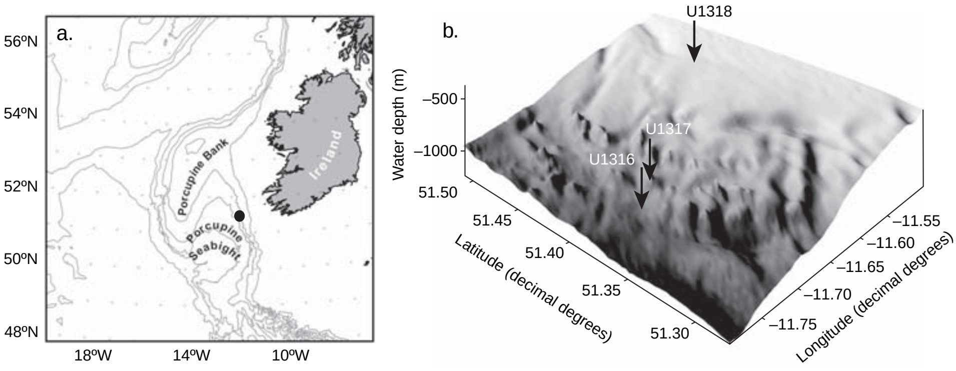


Fig. 4.8. (a) Map showing the location of the Belgica mound province (black circle) in the Porcupine Seabight. (b) Location of holes drilled by IODP Expedition 307. Image (b) modified from Williams *et al.* (2006b), © 2006 American Geophysical Union with permission of the American Geophysical Union.

Case Study 4.1 (cont.)

The base of the mound showed coral rubble overlying a regional angular unconformity (Stoker *et al.*, 2002; Van Rooij *et al.*, 2003; De Mol *et al.*, 2005) with sub-mound sediments revealing a range of dates from 16.58 Ma to 8.96 Ma (Kano *et al.*, 2007), see Fig. 4.9. These Mid-Miocene glauconitic siltstones were firm, but not lithified, suggesting that extensive hardground formation was not necessary for coral settlement and mound initiation. This was despite a significant hiatus in deposition with mound base sediments dated at 2.70 Ma (Kano *et al.*, 2007). It is now clear that from this humble beginning (Fig. 4.10), a large and impressive mound structure eventually developed.

As predicted by hydrocarbon migration models for this part of the Porcupine Seabight (Naeth *et al.*, 2005), elevated concentrations of thermogenic methane (in excess of 6 mM) were found in sandy units tens of metres below the mound base (Fig. 4.11). However, within the mound sequence itself, sub-micromolar

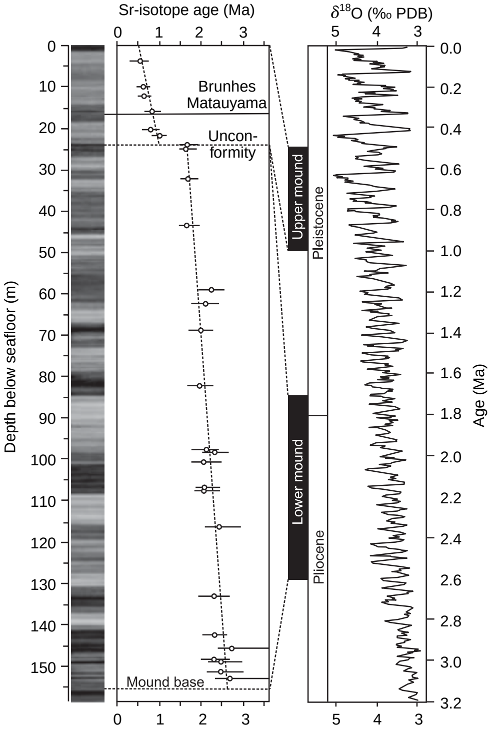


Fig. 4.9. Sediment core image and strontium isotope stratigraphy of mound section of IODP Hole U1317E from the Challenger Mound. Depositional periods of lower and upper mounds are compared with composite benthic $\delta^{18}O$ curve of Lisiecki and Raymo (2005). PDB = PeeDee Belemnite. Modified from Kano *et al.* (2007) with permission of The Geological Society of America.

Case Study 4.1 (cont.)

concentrations were found (Williams *et al.*, 2006b) and prokaryote cell counts, indicating bacterial methane breakdown, fall below the global average (Parkes *et al.*, 2000). Furthermore, the sulfate reduction curve shows minimal perturbations and is generally high, suggesting limited permeability within the mound (Fig. 4.11). There is no evidence of significant methane-derived authigenic carbonate formation. This suggests that although methane exists in strata below the mound, it did not play a role in mound initiation or development and failed to migrate into the low permeability coral carbonate mound sequences with the base of the mound acting as a low permeability cap to vertical hydrocarbon migration. The results from this drilling campaign suggest that the hydraulic theory for mound initiation and development is unfounded in this instance and unable to explain coral carbonate mound formation. Rather, mound initiation 2.7 Ma coincided with the expansion of northern hemisphere ice sheets, the establishment of rigorous interglacial thermohaline circulation and the reintroduction of Mediterranean Outflow Water in the northeast Atlantic (De Mol *et al.*, 2002, 2005; Kano *et al.*, 2007).

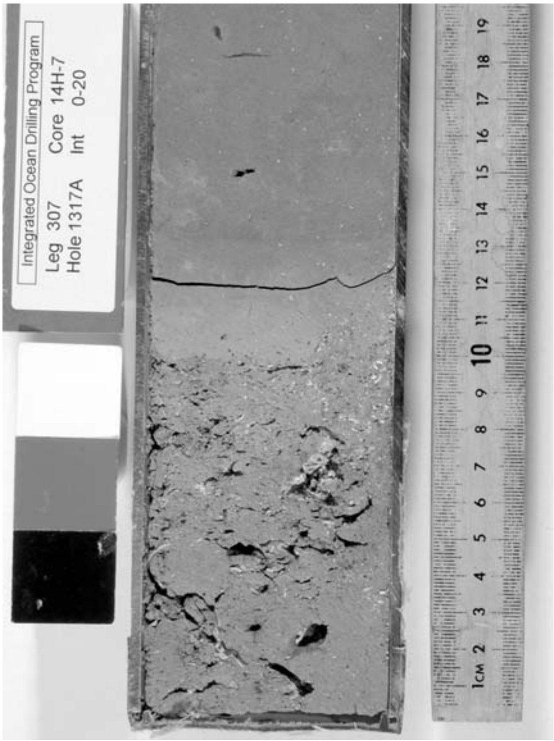


Fig. 4.10. Photograph of the base of core 1317A from Challenger Mound. Image courtesy of the Integrated Ocean Drilling Program.

Case Study 4.1 (cont.)

The internal mound stratigraphy shows apparently continuous mound development with no clear hiatuses from approximately the mound base until 2.7–1.67 Ma (Fig. 4.9). Kano *et al.* (2007) suggest that an increase in glacial intensity after 1.67 Ma may have made conditions sub-optimal for cold-water corals, further reducing mound growth rates. There then follows a significant break in deposition caused by an erosional event with mound growth resuming 1.03 Ma (Sr isotope date: Kano *et al.*, 2007) until 1580–1390 calendar years BP (AMS ^{14}C date). These dates suggest that the lower mound sequences accumulated 15–24 cm per thousand years although after the mound erosional event, growth rates slowed significantly (Kano *et al.*, 2007), which supports the concept of rapid initial growth during an 'active mound' phase (Huvenne *et al.*, 2005).

The mound sequence shows decimetre-scale interglacial or interstadial carbonate and coral-rich intervals alternating with darker glacial clay-rich intervals with

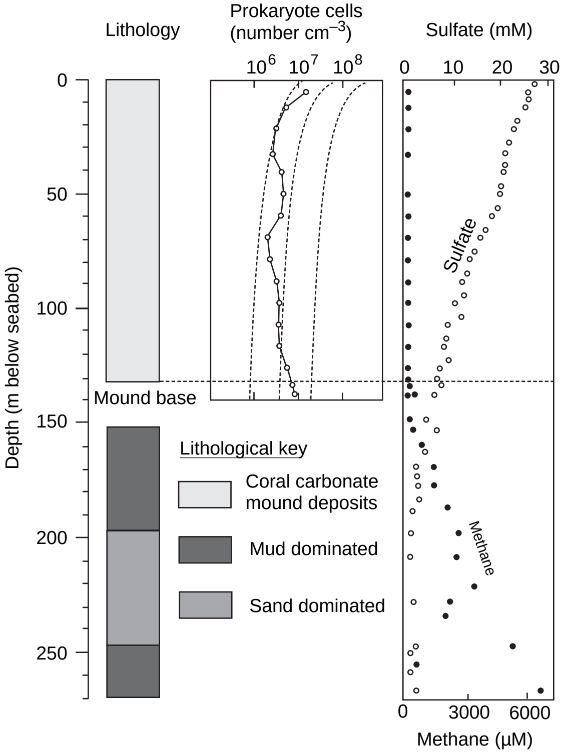


Fig. 4.11. Lithological, microbiological and geochemical variation through Challenger Mound. Data above 140 m are from Hole U1317A (mound base at 133 m), below 130 m from Hole U1317D. Modified from Williams *et al.* (2006b). © 2006 American Geophysical Union, with permission of the American Geophysical Union.

Case Study 4.1 (cont.)

dropstones and better preserved, but sparser, coral remains. Interglacial or interstadial mound growth corresponds to the growth of the framework-forming coral species on Challenger Mound (*Lophelia pertusa* and *Madrepora oculata*), in line with findings from short core sequences from other mounds in this region (e.g. Dorschel *et al*., 2005; Rüggeberg *et al*., 2007).

4.4.2 Mound growth

Seismic imaging of coral carbonate mound bases reveals that most of them cover a broad area (e.g. De Mol *et al*., 2002; Huvenne *et al*., 2003; Colman *et al*., 2005; De Mol *et al*., 2005; Mienis *et al*., 2006; De Mol *et al*., 2007), see Fig. 4.12. Given the scenario of coral carbonate mounds starting from an initial coral settlement site this seems counter-intuitive. Mounds starting from a single initial settlement and growing progressively taller and wider would produce a tapered root to the mound in seismic images. Their broad lateral bases suggest that coral carbonate mounds tend to extend laterally soon after they start to form. This is either because they have high vertical and lateral growth rates compared with off-mound sediment accumulation, and/or they start to form across a broad base at many individual coral settlement sites. Biological growth and sediment trapping by coral frameworks lead one to expect higher sediment accumulation rates on mounds compared with off-mound areas, and studies of sediment accumulation in

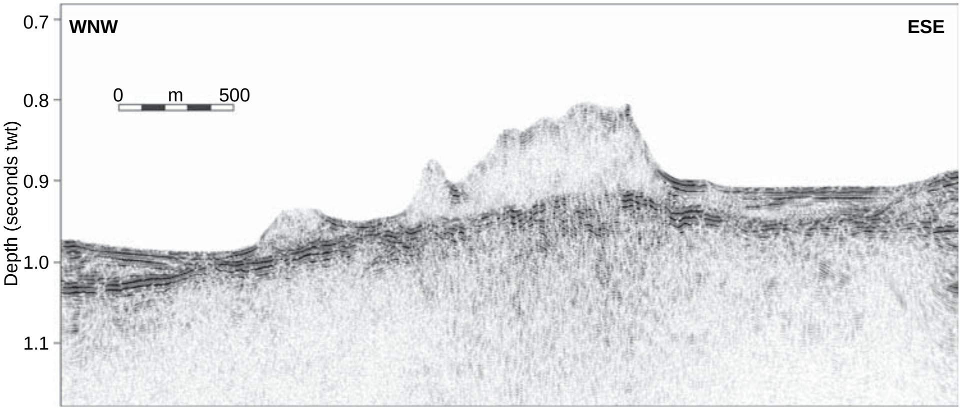


Fig. 4.12. A high-resolution seismic profile through coral carbonate mounds showing broad mound bases on stratigraphic unconformities (a buried seabed erosional surface). A 0.1 second two-way travel time (twt) is approximately 75 m, assuming a sound velocity of 1500 m s^{-1} through the sediments. Seismic line M07II-60 courtesy of H. de Haas.

cold-water coral reefs and mounds support this (see below). The concept of multiple nucleation sites for coral carbonate mounds is also supported by observations that some small cold-water coral thickets and mounds tend to occur in clusters such as the Darwin Mounds (Masson *et al.*, 2003; Wheeler *et al.*, 2008) and the Moira Mounds (Foubert *et al.*, 2005; Wheeler *et al.*, 2005c). Intriguingly, the footprints of Moira Mound clusters are similar to the footprints of the individual giant Belgica mounds implying that these may be precursors of future giant coral carbonate mounds (De Mol *et al.*, 2005).

4.4.3 Accumulation rates

Cold-water coral reefs, at least *Lophelia pertusa* and *Oculina varicosa* reefs, belong to the ‘carbonate factories’ with extremely high sedimentation rates: otherwise one could not explain Holocene reef thicknesses of more than 40 m, such as the Norwegian Fugløy Reef (Lindberg & Mienert, 2005b). In these high latitude settings, reef growth is unlikely to have started before 10 000 years ago, when postglacial oceanic conditions were established (Dahlgren & Vorren, 2003). The oldest radiocarbon ages of *L. pertusa* in Norwegian waters date to 7800–8800 years ago (Mikkelsen *et al.*, 1982; Hovland *et al.*, 1998; Hovland & Mortensen, 1999). This allows a conservative estimation, assuming linear sedimentation rates, of the net accumulation rate of Holocene reefs of up to 4.3 mm yr^{-1} in the case of the 35 m high Sula Ridge reef complex (Freiwald *et al.*, 1999). This rough figure matches well with net accumulation rate calculations of approximately 5 mm yr^{-1} from the Fugløy reef (Lindberg *et al.*, 2007). These astonishingly high sedimentation rates from Norwegian cold-water coral reefs are 10–60 times greater than those estimated from Holocene coral carbonate mound sequences off southwest Ireland, which range from 0.067–0.5 mm yr^{-1} (Frank *et al.*, 2005; Dorschel *et al.*, 2007b; Kano *et al.*, 2007), see Fig. 4.9. The growth rates for *O. varicosa* reefs off Florida, which grow in warmer and more variable temperatures, are not yet fully constrained, but Reed *et al.* (2005) indicate fairly high sedimentation rates of 16 mm yr^{-1}, a value three times higher than that calculated for Norwegian *L. pertusa* reefs.

Cold-water coral reefs and mounds are also enhanced accumulators of carbonate as well as sites with enhanced sedimentation. Carbonate budgets of 54–188 g $\text{m}^{-2}\,\text{yr}^{-1}$ have been derived for Nordic *L. pertusa* reefs, or 0.03–0.38 g $\text{m}^{-2}\,\text{yr}^{-1}$ averaged over the entire Norwegian shelf (Lindberg & Mienert, 2005a). These estimates are considerably lower for the Propeller Mound, Porcupine Seabight, 0.277–5.160 g $\text{m}^{-2}\,\text{yr}^{-1}$ (Dorschel *et al.*, 2007b), reflecting lower sedimentation rates and periodic hiatuses. This suggests that cold-water corals may contribute to $>1\%$ of total marine calcium carbonate production (Lindberg & Mienert, 2005a). These rates are significantly lower than those estimated for tropical coral reefs but remain high when compared with other sedimentary settings in temperate latitudes. Therefore cold-water coral reefs and coral carbonate mounds represent significant carbonate production centres at these latitudes.

4.4.4 Climatic controls on mound growth

Reef growth continues until external factors, such as climate-induced variations in environmental conditions and sedimentation rate curtail reef growth (Fig. 4.2). Fundamental changes occur in the marine environment when climate shifts from interglacial to glacial conditions (Fig. 4.13). Water temperatures diminish and current speeds slow, reflecting an overall reduction in ocean circulation, but sediment supply increases. This increase may come from several sources: (1) direct glacio-marine sources if the reefs/mounds are close enough to the ice front; (2) enhanced fluvio-glacial across-shelf sediment supply assisted by lowered global sea-level moving coastlines onto the present shelf, or even to the present shelf break so exposing interglacial shelf sediments to erosion; and (3) from melting icebergs producing ice-rafted debris. Most ice-rafted debris is fine-grained clay to silt, although icebergs can transport boulder-size material into deep marine settings supplying an important mechanism to provide substrata for coral colonisation during later interglacial and interstadial periods (Colour plate 14).

Providing the dead coral structure exists at depths beyond glacial scouring, it will not be removed by advancing glaciers. Instead the coral structure forms an obstacle that continues to collect sediment until the old reef frameworks are completely buried (Fig. 4.2e). Even after this, sedimentation may continue covering the mound in a mantle of glacio-marine deposits. Some coral species may continue to grow through this harsher regime. The new accumulation of sediment may be prone to slumping and erosion as current speeds accelerate at the start of the following interglacial cycle (Dorschel *et al.*, 2005; Rüggeberg *et al.*, 2007). The return of interglacial climatic conditions will allow new coral generations to grow on the now fossil, pre-existing reef, or on dropstones exposed after flank erosion or slumping (Dorschel *et al.*, 2005), forming a coral carbonate mound structure.

Changes between warm and cold climates have occurred many times in the northern hemisphere over the past 3.5 Ma (Bartoli *et al.*, 2005). Following this line of reasoning, a mound represents several coral reef sequences in a stacked pattern. The coral carbonate mound provides positive modifications to the seabed environment in comparison with off-mound settings and experiences more rigorous hydrodynamics and isolation from smothering bedload transport. Thus, conditions on-mound become more favourable to colonising fauna and further enhance reef

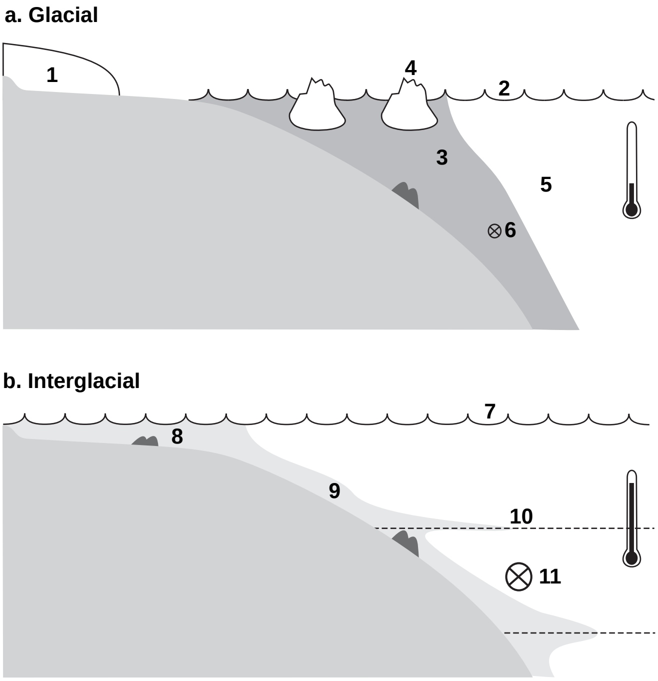


Fig. 4.13. Schematic diagram illustrating differences between interglacial and glacial environmental conditions. (a) Glacial conditions with cooler ocean temperatures and (1) ice prograding onto the shelf exposed due to (2) low eustatic sea levels. (3) Glacio-marine sediment supply to the continental margin is high with additional (4) ice-rafted debris. (5) Water masses are unstratified and (6) along-slope currents are weak. (b) Interglacial conditions with warmer ocean temperatures and (7) high eustatic sea levels flooding continental shelves where (8) cold-water coral reefs may form. (9) Sediment supply is lower but may become concentrated in (10) nepheloid layers in a more stratified ocean. (11) Along-slope currents are stronger.

development. Dense coral frameworks in interglacial and interstadial intervals may provide internal stability to the mound sequences, crucially underpinning vertical mound growth and allowing mounds, and perhaps some fauna, to persist.

At the time of writing, new information was becoming available on the timing of reef development at low-latitude coral carbonate mounds where glacial and interglacial periods are characterised by changes in upwelling and terrestrial aridity (Martinez *et al.*, 1999; Zhao *et al.*, 2003). In the Banda Mound province off Mauritania, isotopic dates suggest that *Lophelia pertusa* seems to grow preferentially during glacial periods at a time when temperate latitude reef development is rare (M. Eisele, personal communication, 2008). On the New England seamounts in the northwest Atlantic, the large pseudocolonial scleractinian *Desmophyllum dianthus* is more abundant in glacial periods. This

Topic box 4.2 **Calcium carbonate mineralogy**

Calcium carbonate ($CaCO_3$) is a common component of seafloor sediments. It can be directly precipitated from seawater, or pore fluids within the sediment or secreted by organisms, like cold-water corals, which may then contribute calcium carbonate to the seafloor sediment in the form of their skeletal remains. The atoms that make up the calcium carbonate molecule can be arranged in two crystal habits defining two different minerals or polymorphs: calcite and aragonite. Calcite is a colourless to white crystal (occasionally grey, yellow or green) with a trigonal-rhombohedral crystal habit (the fundamental structural unit of the crystal is rhombus-shaped with sides of equal length). Calcite is the most stable crystal polymorph of calcium carbonate. Aragonite has an orthorhombic crystal habit (best visualised as a ‘stretched cube’). Cold-water scleractinian corals produce aragonite skeletons that are stronger than calcite but less stable. Aragonite goes into solution at shallower depths than calcite and geological aragonitic remains and cements are likely to recrystallise into calcite (a process known as inversion).

The magnesium atom easily substitutes for calcium in the calcite crystal lattice. This gives rise to a new mineral, high-magnesium calcite, that has the same crystal structure as calcite but with variable, greater than 4 mol% magnesium. This can be both precipitated inorganically and biomineralised, for instance by cold-water coral reef organisms like echinoderms, benthic foraminiferans and bryozoans. Over time, the diagenetic substitution of calcium for magnesium in calcium carbonate may give rise to the mineral dolomite, $CaMg(CO_3)_2$. This process of dolomitisation affects cold-water coral mound sediments and sediment components. Dolomitisation destroys the original sedimentary and biological microstructures and increases porosity within the sediments.

species seems to thrive during periods of rapid climate change but it is not yet known why *D. dianthus* growth on the New England seamounts should be linked with glacial periods (Robinson *et al*., 2007).

4.4.5 Diagenetic processes

This section describes the conversion of unconsolidated coral carbonate mound sediment into hard limestone through synsedimentary lithification, or early diagenesis. Compared to the plethora of diagenetic processes known from shallow-water reef sediments, the lithification of deep-water limestones remains relatively poorly studied.

The stages of coral carbonate mound diagenesis are illustrated in Fig. 4.14. The initial stage is sediment compaction and de-watering under the weight of

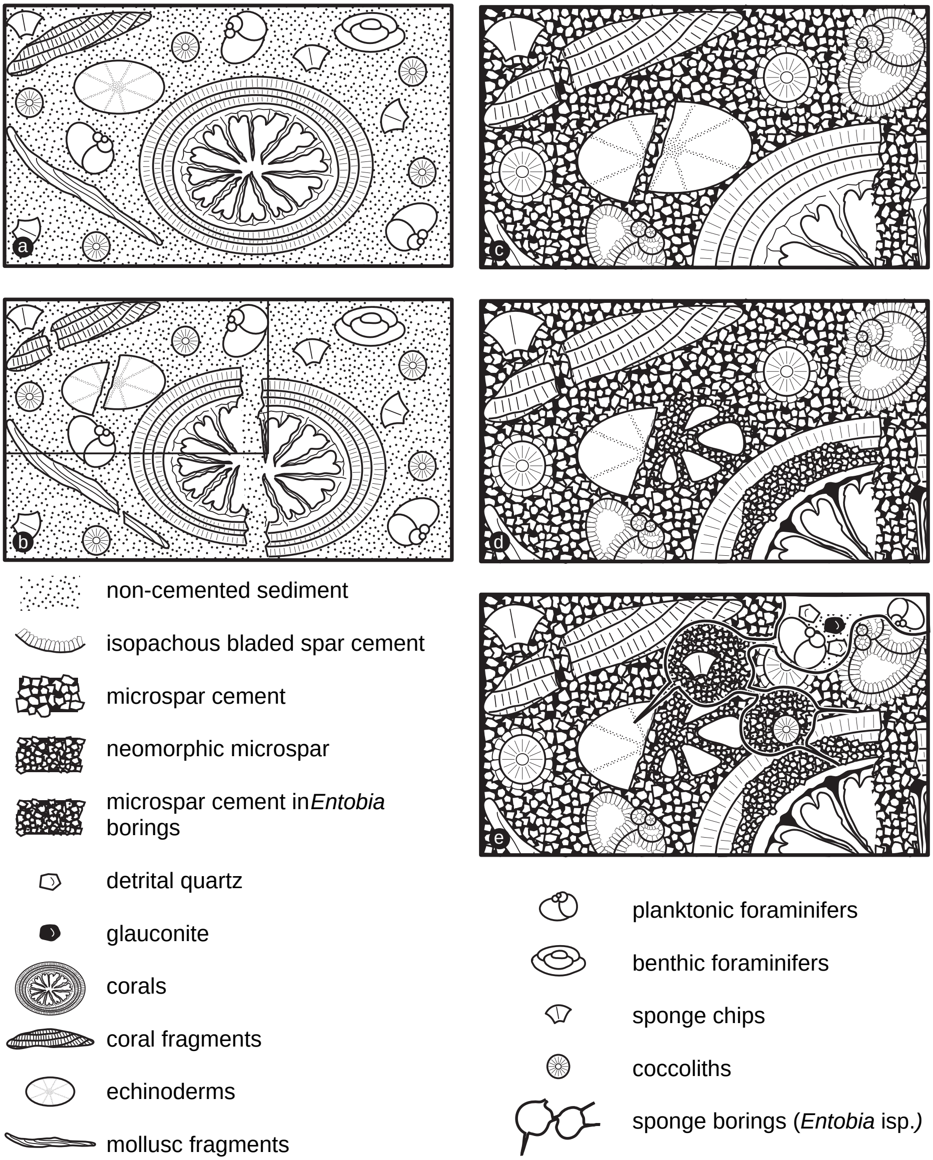


Fig. 4.14. Schematic diagram showing the sequence of coral carbonate mound diagenesis. (a) Typical coral carbonate mound sediment. (b) Sub-surface stage I: physical compaction. (c) Sub-surface stage II: rim and spar cementation. (d) Sub-surface stage III: neomorphism. (e) Seafloor stage II: exhumation and hardground formation. Coccoliths are not shown to scale. Dissolved centres of calcification are shown in black. Box in panel (b) is enlarged on panels (c–e). Reproduced from Noé *et al.* (2006) with permission of Springer Science +Business Media.

overlying sediments. This reduces porosity and may also result in crushing or breaking of brittle bioclasts (Noé *et al.*, 2006). Soon after deposition, calcitic microspar starts to form in the rims of foraminiferal tests and may completely infill them (Fig. 4.15). Microspar forms the most important and pervasive type of cement in cold-water coral limestones. In former pelagic and hemipelagic muds, microspar cement produces a fine crystalline groundmass of equal-sized euhedral or subhedral calcite crystals with grain sizes 5–10 μm (see Topic box 4.2). According to Folk (1974), calcareous mud consisting of aragonite and calcite turns into calcite although the calcite crystals will grow no larger than 2–3 μm. Scleractinian skeletons, pteropods or other aragonitic material imported from shallow-water carbonate platforms provide a source of carbonate ions (CO_3^{2-}) for cementation. Aragonite skeletons undergo either variable degrees of dissolution (Titschack & Freiwald, 2005) or experience inversion to calcite, a process called neomorphism. More specifically, calcitic microspar formation derives from inversion of aragonite and dissolution–reprecipitation processes (Mazzullo, 1980). The plates of coccoliths, which form the bulk of pelagic ooze material, are preferred microspar nucleation sites (Fig. 4.16). From here microspar grows into unfilled primary inter-particle pore space (Noé *et al.*, 2006). The degree of microspar cementation is inversely proportional to the abundance of sand-sized or larger bioclasts in the sediment: the smaller the grain size of the sediment, or the greater the density of coccoliths, the lower the level of cementation. This explains the friability of pure, fine-grained chalk.

Nanoplankton oozes have low permeability (Scholle & Ulmer-Scholle, 2003) that impedes pore water flux through the sediment and so limits carbonate ion transport to the nucleation sites of cementation. This can cause differential cementation of cold-water coral sediments making their lithification patchy (Noé *et al.*, 2006). Sediments rich in sand-sized bioclasts, on the other hand, possess a higher primary porosity and permeability, allowing for free pore water flux and active ion transport that accelerates microspar cementation.

Hardgrounds may also form where lithification is only occurring at the seabed or in the shallow sediment sub-surface below loose surface sediments. Hardground formation is assisted by strong currents flowing over the exposed coral carbonate mound sediments. These strong currents enhance carbonate ion diffusion from seawater through the surface sediments promoting hardground formation *in situ*. Currents may also erode loose sediments exhuming deeper lithified substrata and exposing them as hardgrounds. Either way, hardgrounds indicate gaps in sedimentation, are often coated by iron–manganese precipitates (Allouc *et al.*, 1999) and allow a sessile community to colonise on or bore into the hardground crust.

The degree of cementation depends on the sediment composition controlling the sedimentary fabric, primary porosity and permeability and on near-seabed

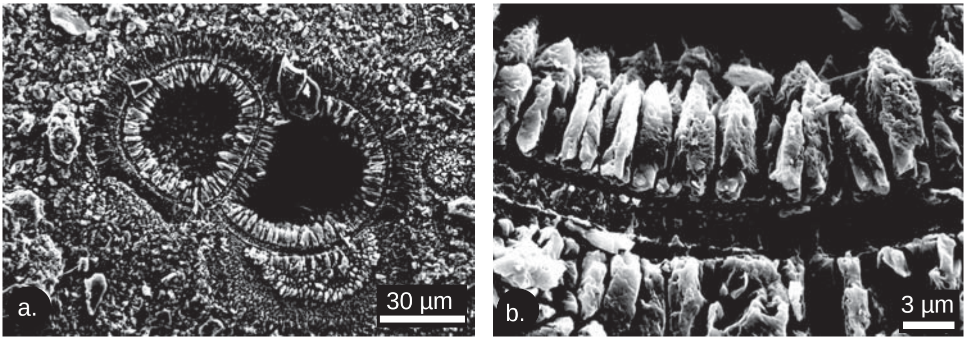


Fig. 4.15. (a) Microspar growth on both sides of the rims of foraminiferal tests as the first stage in diagenetic crystallisation of coral carbonate mound sediments. (b) Close-up showing isopachous-bladed spar consisting of euhedral crystal arranged at 90 degrees to the foraminiferal test rim. Modified from Noé *et al.* (2006) with permission of Springer Science+Business Media.

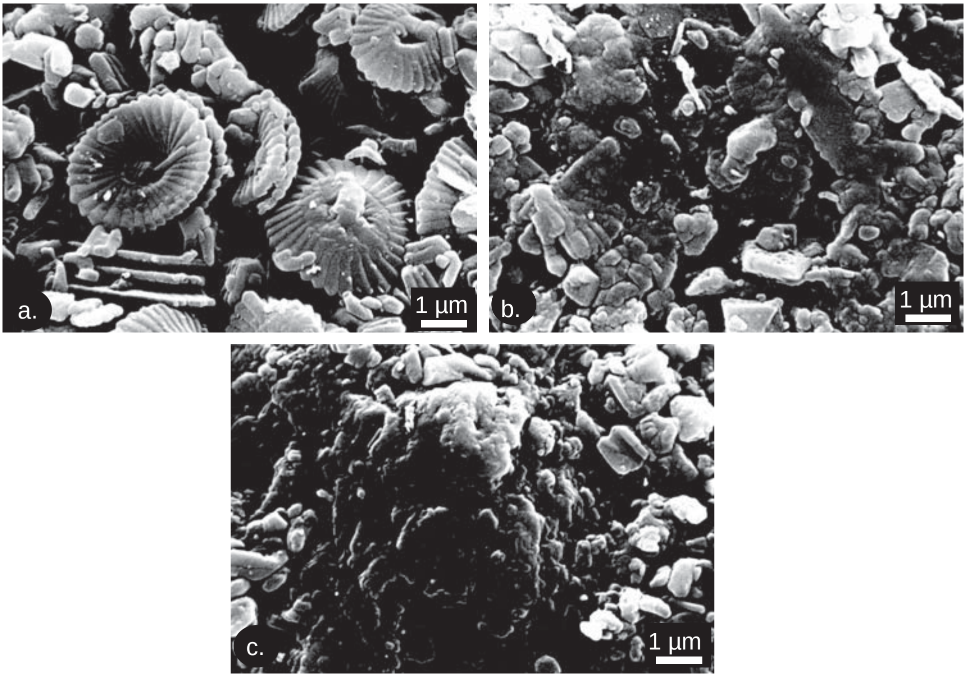


Fig. 4.16. Progressive microspar cementation of cold-water coral ooze. (a) A scanning electron micrograph showing *Gephyrocapsa* sp. coccolithophorids. The specimen in the bottom right shows syntaxial cement overgrowth by microspar of the central pore. (b) Massive syntaxial overgrowth with euhedral and anhedral microspar crystals interlocking. (c) Complete incorporation of coccoliths in microspar. Modified from Noé *et al.* (2006) with permission of Springer Science+Business Media.

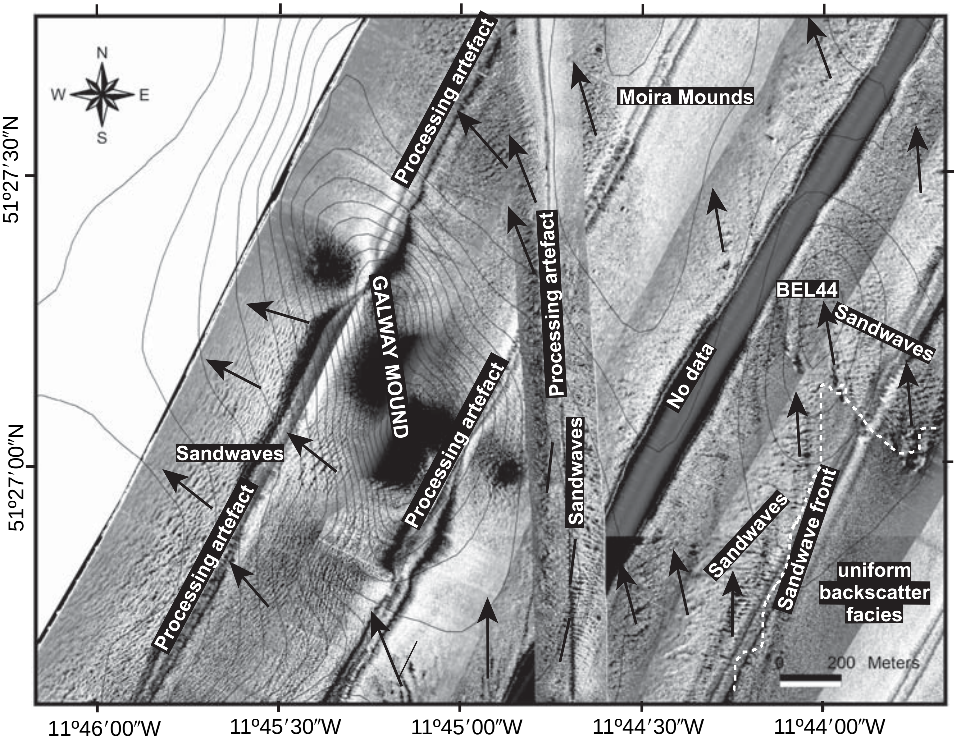


Fig. 4.17. A 100 kHz side-scan sonar mosaic with a 410 kHz overlay in the Galway Mound and BEL44 coral carbonate mounds area showing sandwave fields and small solitary Moira Mounds. Black arrows show bedload transport directions interpreted from bedform asymmetry that flow around the obstacles formed by the mounds. Off-mound conditions vary from uniform backscatter facies (typified by rippled sands) to sandwaves formed by faster benthic currents. Figure reproduced from Dorschel *et al.* (2007a) with permission of Elsevier.

current velocity that drives the pore water flow (Melim *et al.*, 2002; Noé *et al.*, 2006). In such diagenetic regimes aragonitic fossils, such as scleractinian corals, are generally dissolved and are preserved as moulds, or become inverted to a calcitic mineralogy. Preserved aragonitic cold-water corals are mostly recorded from hemipelagic sediments where the skeletons were sealed in muds and protected from dissolution by low pore-water exchange rates. Examples are known from the Palaeocene Sobral Formation of Antarctica with preserved aragonitic *Madrepora sobral* and from the Early Pleistocene Saint Paul's Bay Limestone on Rhodes, eastern Mediterranean Sea, with pristine *Lophelia pertusa* and *Madrepora oculata* (Filkorn, 1994; Titschack & Freiwald, 2005; Titschack *et al.*, 2005), see Case study 6.1, p. 190. Such pristine coral skeletons are unique environmental archives of palaeoproductivity, ocean circulation, ventilation and climate (see Chapter 7).

4.4.6 Late-stage mound development and burial

As the mound grows bigger two key situations start to develop. Firstly, the mound summit may become increasingly isolated from bedload transport that can no longer migrate up the sides of the mound, especially true if the mound is covered by dense coral cover. This means that the supply of lithic sediment is reduced compared to hemipelagic sediment input. This restriction in sediment supply will reduce the rate of mound growth. Secondly, the mound will form an obstacle to currents, altering near-mound flow fields (see Fig. 4.17) and generating its own mound-specific hydrodynamics (Wheeler *et al*., 2005c; White *et al*., 2005; Dorschel *et al*., 2007a; Wheeler *et al*., 2007) with increased elevation making the mound more susceptible to erosion. A mound may even grow so high that any further growth would place its summit in a different water mass less conducive to coral growth. The mound then becomes increasingly embedded within sediment drifts whose vertical accumulation rates now outstrip that of the mound's own growth. Encroachment of drift deposits on coral carbonate mounds is recorded in the Belgica mound province (Van Rooij *et al*., 2003, 2007a, b) and ultimately this may result in mound burial of which there are numerous examples from seismic surveys (e.g. Huvenne *et al*., 2003, 2007; Van Rooij *et al*., 2008), see Fig. 4.18.

4.5 Coral carbonate mound morphology

Coral carbonate mounds form a variety of shapes and sizes reflecting both different stages of development and morphological responses to environmental controls on growth processes. With increasing multibeam echosounder coverage (see Section 1.2.1, p. 13) of areas of coral carbonate mounds and high-resolution digital terrain models (Colour plate 5), mound morphologies can be resolved with greater resolution and certainty. Deep-tow high-frequency multibeam and side-scan sonar mapping can also reveal high-resolution reef and mound surface morphologies (Wheeler *et al*., 2007), see Colour plate 5 and Fig. 4.19. Multibeam maps can be manipulated using spatial statistical packages in geographical information systems (GIS) to examine reef and mound dimensions (e.g. De Mol *et al*., 2005; Fosså *et al*., 2005; Wheeler *et al*., 2007). Buried mounds can also be resolved with three-dimensional seismic data (Huvenne *et al*., 2003; Colman *et al*., 2005).

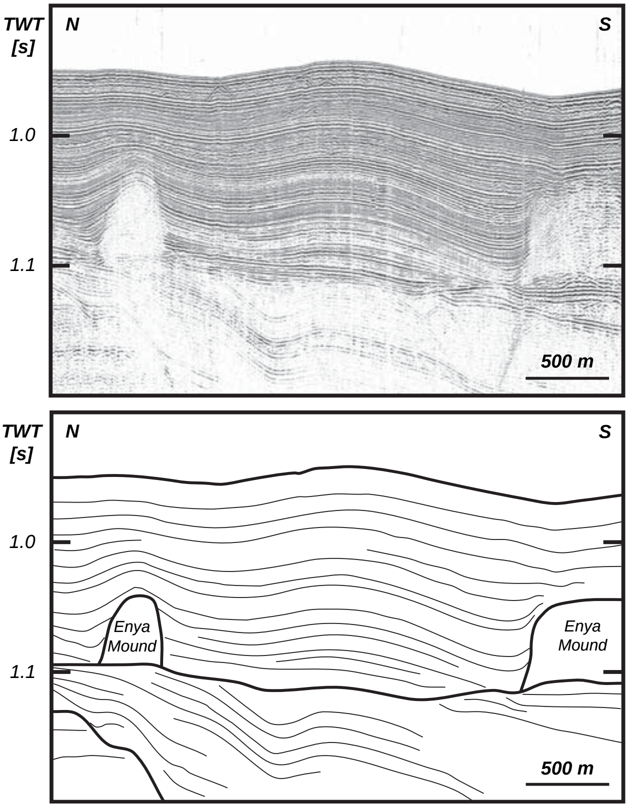


Fig. 4.18. The Enya Mounds are examples of buried coral carbonate mounds entombed in drift sediment. Modified from Van Rooij *et al.* (2008) with permission of Springer.

4.5.1 Mound shape

Colour plate 16 shows a variety of coral carbonate mounds and reefs resolved by multibeam mapping. On the mound surface, reef morphology tends to reflect biological growth forms (essentially the coral colony morphology) and (bio)erosion: ‘cauliflower-like’ (e.g. on the Sula Ridge: Freiwald *et al*., 1999) and ‘undulating’ shapes due to coral ridge formation are both noted (e.g. Wheeler *et al*., 2005c), see Colour plate 15 and Fig. 4.19. Morphology of the entire mound also varies, with a conical mound representing an idealised shape whereby the mound simply grows upwards at the summit and spreads outwards towards the base. Conical mounds are relatively rare, while ridge-shaped mounds are more common. Wheeler *et al*. (2007) review variation in northeast Atlantic coral carbonate mound morphology and note the importance of environmental controls on mound development with current-aligned ridge morphologies being common.

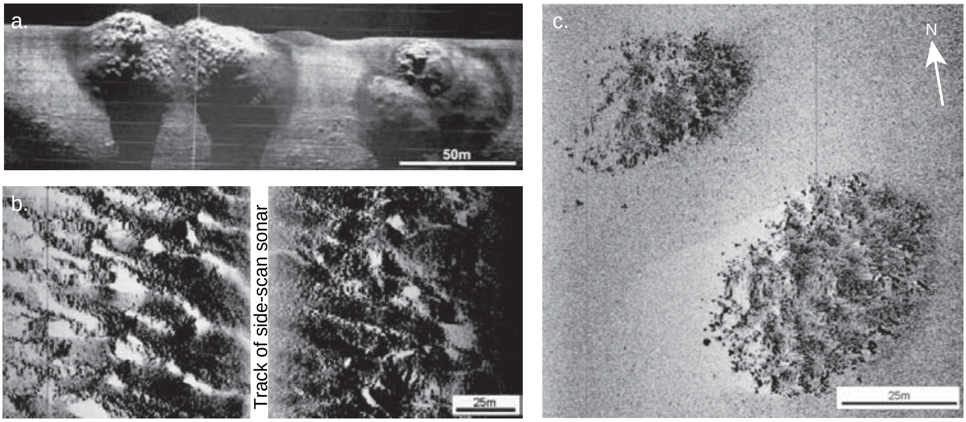


Fig. 4.19. (a) Surface morphology of the Sula Ridge showing circular reefs with a 'cauliflower-like' morphology reflecting the shape of individual colonies (500 kHz side-scan record modified from Freiwald *et al.*, 2002). (b) Surface morphology of the lower flanks of the Galway Mound showing undulating morphologies due to coral ridge formation (410 kHz side-scan record from Wheeler *et al.*, 2005c). (c) A small discrete coral thicket showing a random arrangement of coral colonies from the Darwin Mounds, north Rockall Trough, northeast Atlantic (410 kHz side-scan record from Wheeler *et al.*, 2008). Images (a) and (b) reproduced with permission of Springer. Image (c) reproduced with permission of the International Association of Sedimentologists and Blackwell Publishing.

They describe two types of mound morphology: 'inherited' and 'developed'. Inherited morphologies reflect the topography of the initially colonised substrata and are more conspicuous with small mounds. As mounds grow their morphology will become developed in response to the influences of prevailing current direction, sediment supply and scouring. Furthermore, if coral carbonate mounds are closely spaced they may grow into one another, developing into a complex mound cluster.

4.5.2 Mound dimensions

The Irish seafloor has the best-studied coral carbonate mounds, including some of the largest examples (Logachev Mounds). These are the most extensively mapped of all coral carbonate mounds, although comparable mapping detail is now emerging from the Straits of Florida (Grasmueck *et al.*, 2006). Spatial relationships between coral carbonate mounds and their dimensions have been analysed for individual mound provinces using regional mapping data (Beyer *et al.*, 2003; Huvenne *et al.*, 2003; O'Reilly *et al.*, 2003; Wheeler *et al.*, 2007). With a newly

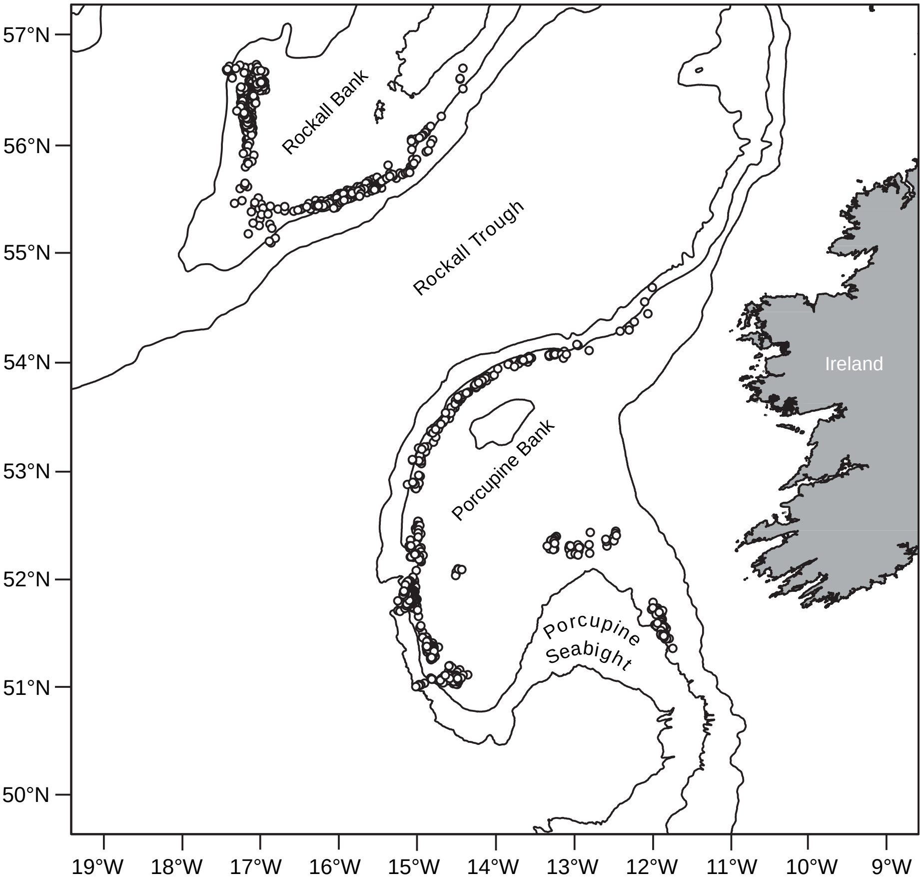


Fig. 4.20. Distribution of verified coral carbonate mound provinces on the Irish seafloor. Figure courtesy of B. Dorschel.

available comprehensive multibeam echosounder dataset of the whole Irish seafloor (525 000 km^2), recent studies (B. Dorschel, personal communication, 2008) summarised here show that it is now possible to assess the spatial relationships and dimensions of all mounds in Irish waters (Fig. 4.20).

As can be seen in Fig. 4.20, cold-water coral carbonate mounds accumulate along the slopes of Rockall Bank, Porcupine Bank and the eastern Porcupine Seabight. Analyses of the depth distribution of the mound summits highlight these vertical distribution patterns (Fig. 4.21) revealing a trend skewed towards shallower water depths with a dominant frequency of mounds occurring around 625 m water depth. The cumulative distribution curve shows that 90% of mound summits occur in water depths <860 m with two-thirds of the mound summits located <720 m water depth. The asymmetry of the differential distribution

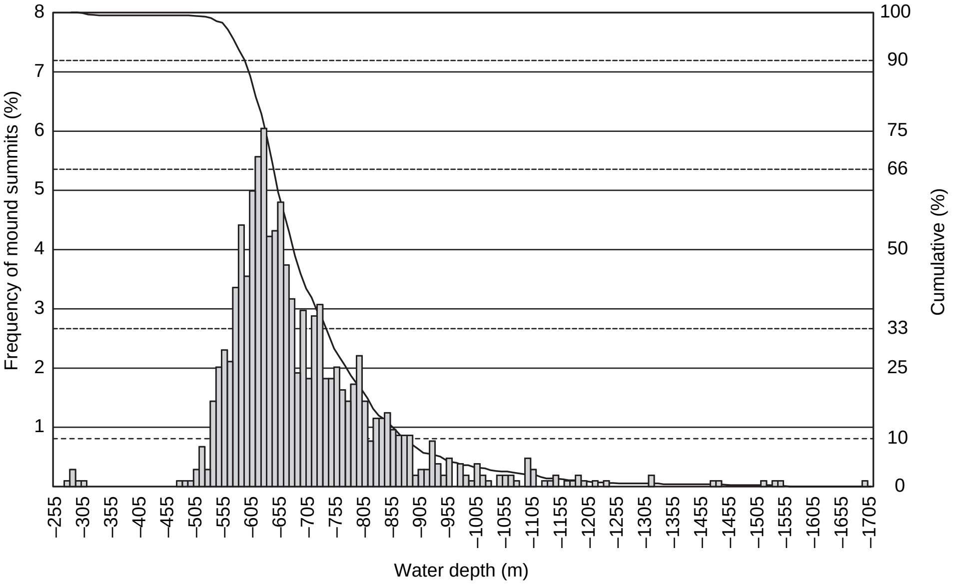


Fig. 4.21. Depth distribution of summits of verified cold-water carbonate mounds on the Irish seafloor. Bin size for mound frequency is 10 m water depth. Figure courtesy of B. Dorschel.

could indicate an upper growth limit for coral carbonate mounds. This tendency becomes even more pronounced when comparing mound heights with the vertical distribution patterns of mound bases on the seafloor (Fig. 4.22). The wedge-shaped distribution with larger mounds located in deeper waters further supports the hypothesis of an upper growth limit for coral carbonate mounds.

4.6 Global distribution of coral carbonate mounds

Distributional data for cold-water corals are usually derived from information on species occurrence. Ancillary information on whether a reef or coral carbonate mound is present is less frequently available. At the time of writing, the known distribution of coral carbonate mounds is even more restricted than that of cold-water coral reefs (see Fig. 4.23) and shows these features confined to the upper and mid-slopes of continental margins such as the Porcupine Seabight, the Gulf of Cadiz, the Moroccan margin, the Mauritanian margin, the Florida-Hatteras Strait, Blake Plateau, eastern USA and Gulf of Mexico (Newton *et al.*, 1987; Colman *et al.*, 2005; De Mol *et al.*, 2005; Grasmueck *et al.*, 2006). The bathyal flanks of larger oceanic banks such as the Chatham Rise, West African seamounts, Hatton, Rockall and Porcupine Banks are also preferred sites for coral carbonate mound formation, and many more must surely await discovery.

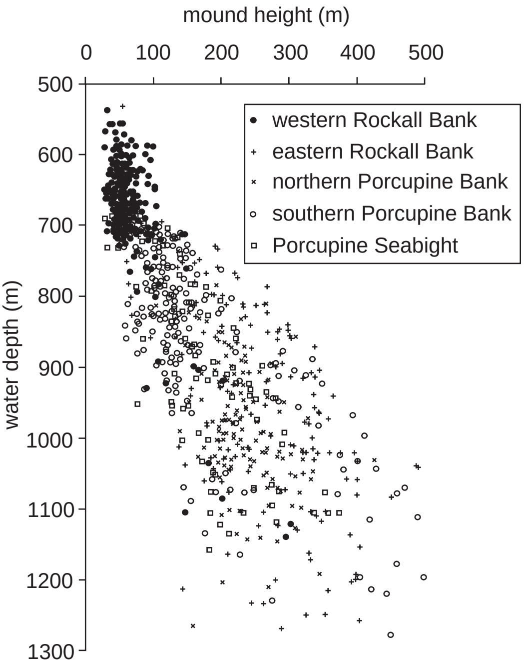


Fig. 4.22. Coral carbonate mound height plotted against water depth of the mound base showing mound provinces with similar depth–height relationships. Note also that deeper mounds have a greater variation in mound height but also a capacity to grow bigger, nevertheless not growing shallower than about 600 m water depth. Figure courtesy of B. Dorschel.

Cold-water coral reefs as defined in Chapter 2 (see Topic box 2.1, p. 23) and exemplified by the *Lophelia pertusa* reef habitats of the Norwegian continental shelf represent Holocene systems that have developed apparently continuously since the end of the last glaciation. The typically larger coral carbonate mounds form over millions of years and represent sites of repeated cold-water coral reef formation. The global distribution of these mounds can therefore be viewed as marking sites particularly favourable to cold-water coral reef growth during the Pleistocene and Late Neogene (Cenozoic). Although the number of locations shown on Fig. 4.23 is limited, each of these areas contains many mounds. Paull *et al.* (2000) estimated that up to 40 000 lithoherms are present in the Florida-Hatteras Strait and 1042 have been identified in Irish waters (B. Dorschel, personal communication, 2008).

At high latitudes where cold-water corals tend to be in shallower waters coincident with appropriate seawater temperatures there are many cold-water coral reefs but few coral carbonate mounds. Reefs formed at these latitudes are more likely to be eroded during glaciations when ice sheets and glaciers not only extended to lower latitudes but also, with global sea level 120–130 m lower than

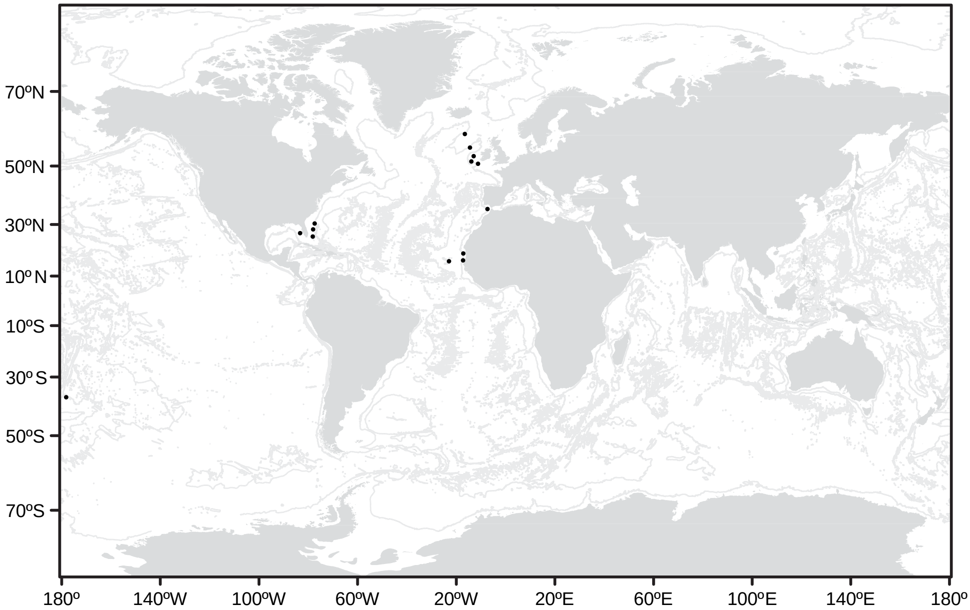


Fig. 4.23. Global distribution of known coral carbonate mounds. The distribution is an underestimate as in many cases it is not clear if reef structures not shown have in fact grown successively at the same site and are therefore true coral carbonate mounds. In other cases, it is not clear if topographically elevated reefs have colonised rock outcrops or have generated their own topography through mound development. The distribution is also clearly skewed by an Atlantic survey bias in work carried out to date.

today (Labeyrie *et al*., 1987; Fairbanks, 1989), many of the continental shelves where these northerly reefs are now found were not even submerged. The tendency for coral carbonate mounds to occur at mid-latitudes rather than deep-water tropical latitudes probably reflects the coincidence of water masses commonly occurring in the appropriate temperature range with sites on continental margins frequently experiencing strong currents and high food supply (Freiwald, 2002; Kenyon *et al*., 2003). Continental margin settings may also experience hydrodynamic conditions beneficial for cold-water coral growth such as internal tides and waves that may be important in supplying food particles to the corals and other animals that live among them (see Section 3.3.2, p. 77). We return our attention now to the importance of cold-water corals as habitat-forming organisms and consider their ecology and significance as local centres of faunal biodiversity.

5

Habitats and ecology

> *In a band somewhat restricted in depth, extending downwards from the 100-fathom line, we met in some places with very large numbers of many varieties of* Caryophyllia borealis*, FLEMING; and at depths of 300 to 600 fathoms the handsome branching* Lophohelia prolifera *PALLAS forms stony copses covering the bottom for many miles, the clefts of its branches affording fully appreciated shelter to multitudes of* Arca nodulosa, Psolus squamatus, Ophiopholis aculeata *and other indolent 'commensals'.*
>
> *The Depths of the Sea*
> Charles Wyville Thomson (1874)

The habitat-forming capacities of corals have fascinated generations of marine biologists. Shallow-water tropical coral reefs, so often called the 'rainforests of the sea', are home to the greatest vertebrate biodiversity on the planet with over 4000 species of reef fish in 179 families estimated to be found in the Indo-Pacific region alone (Myers, 1989). The ability of one species to provide habitat for others has been formalised through the concept of 'ecological engineering' (Jones *et al.*, 1994; Wright & Jones, 2006) and we discuss this in relation to cold-water corals and some of their symbiotic associates later in this chapter. Different cold-water coral species develop habitats of varying physical sizes and life spans. For instance, gorgonians may grow close together, forming dense forest-like habitats, but after death these colonies will break down, unlike the reef frameworks left by colonial scleractinians that were discussed in the last chapter. The skeletons of long-lived cold-water corals, like the precious, bamboo and black corals, can themselves provide structural habitat during their lifetimes that may also persist for some time after death. The diversity of attached invertebrates on a newly discovered species of large white antipatharian coral from the southern California Bight was so striking that it was named *Antipathes dendrochristos*, or the Christmas tree coral, because the attached epifauna looked like ornaments hanging from a snow-covered

Topic box 5.1 **Biodiversity**

The number of species or the richness of a community is often simply referred to as its diversity or its biodiversity. But in the real world, and in the deep sea in particular, it is impossible to sample, identify and count all the species present in a community. So species richness must be estimated by sampling the community, and this immediately introduces a problem. Say a community is composed of 100 000 individuals made up from 10 species. If each species is represented evenly with 10 000 individuals apiece, each equally likely to be sampled, then randomly sampling 1000 individuals from this community (1%) will return an accurate picture of its species richness. But if the number of individuals is not evenly distributed between species so that some species dominate the community while others are rare, then a random sample from this community may not reflect the true number of species present. To overcome this, species diversity estimates should ideally consider both the *richness* (number of species present) and the *evenness* with which the individuals are distributed between species.

Biodiversity may be thought of in various ways:

1. **Alpha diversity** (α) is the number of taxa (e.g. species, genera, etc.) within a certain area or ecosystem; usually expressed as the number of taxa present ('local diversity').
2. **Beta diversity** (β) refers to the variation in community composition between areas; usually measured as the change in taxa between areas or ecosystems or along spatial and environmental gradients ('turnover diversity').
3. **Gamma diversity** (γ) is the overall diversity of a large area ('regional diversity').

Ecologists have developed an array of statistical indices to describe these differing views of biodiversity. A popular index, often appropriate in deep-water ecosystems with many rare species, is the Shannon–Wiener index (H'):

$$H' = -\sum p_i \ln p_i \qquad \text{(Eq. 5.1)}$$

Where p_i is the proportion of individuals found in the ith species. This index assumes that individuals are sampled from an effectively infinite population and that all species are represented in the sample. The latter assumption is probably rarely met and introduces an error that increases as more species are missed from the sample. See Gage and Tyler (1991) and Magurran (1988) for further discussion.

Christmas tree (Opresko, 2005; Yoklavich & Love, 2005) – a subsequent study of a dead colony of *A. dendrochristos* found over 2500 individual animals dominated by corophioid amphipods, sea anemones, brittle stars and crinoids (Love *et al.*, 2007).

The complex three-dimensional architecture and spatial variability of cold-water coral habitats seems integral to providing varied niches for the members of their species-rich communities, but these structural habitats resist conventional deep-sea sampling equipment (see Section 1.2.3, p. 15), limiting our understanding of biodiversity patterns. Conventional box corers are designed for muddy deep-sea abyssal sediments and, while they can be used on cold-water coral reefs, coral can often wedge open the spade designed to seal the core and the sample may partially wash away while being brought back through the water column. Large structural corals, like the *A. dendrochristos* skeleton discussed by Love *et al.* (2007), are hard to recover intact and many associated animals simply detach or swim away when the colony is lifted from the seabed. Finally, many, if not all, of the community ecology studies to date have been biased both by collection method and the taxonomic expertise applied with further biases towards the best known groups. For example, species from taxonomically challenging groups, such as sponges, are often poorly represented in studies of faunal diversity from cold-water coral habitats (see van Soest *et al.*, 2007).

But despite these difficulties we are learning more about the importance of cold-water coral habitats for species richness, or 'alpha diversity', and are beginning to see the significance of species turnover between habitats, or 'beta diversity' (see Topic box 5.1). This chapter highlights the ecological significance of major reef habitat types introduced in Chapter 4 and considers the structural habitats provided by other cold-water corals. We include specific case studies of cold-water coral habitats that have been described in some detail and, thanks to ecological studies of recent years, summarise what has been discovered about species interactions from mutualistic symbiosis to predator–prey interactions and the significance of cold-water coral habitats for fish populations.

5.1 Habitats

Before considering the variety of habitats and species in more detail it is worth pausing to define some terms and make an important distinction between coral habitats and habitats *provided* by corals. We will follow the terminology defined by Fauth *et al.* (1996) where a community is simply 'a collection of species occurring in the same place at the same time' and assemblages refer to 'phylogenetically related groups within a community'. The simplest definition of a habitat, the location or environment where an organism lives, may not relate well to the great variety of spatial scales a habitat can cover, an especially acute issue for marine habitats in waters >200 m deep. We therefore follow the approach of Greene *et al.* (1999) whose deep-sea habitat classification scheme is a practical way of categorising habitats like cold-water coral reefs where our understanding of their boundaries and scale is often based on remotely sensed geophysical information (see Section 1.2.2, p. 14).

At the largest scale, megahabitats are features with dimensions from kilometres to tens of kilometres. Important megahabitats for cold-water coral habitats include canyons (Colour plate 18), seamounts, offshore banks and mid-ocean ridges. Mesohabitats have dimensions from tens of metres to a kilometre and would include smaller seamounts, banks and canyons as well as reefs (and coral carbonate mounds), glacial moraines, lava fields, overhangs and bedrock outcrops, all of which might be important for cold-water coral habitats. Macrohabitats are defined as from one to ten metres in scale and include boulders, rocky reefs, bedrock outcrops and biogenic structures such as cold-water coral reefs. To this list we add microhabitats provided within the complex architecture of cold-water corals and their skeletal remains.

It is also worth noting that much of the available literature on cold-water coral habitats comes from geological mapping investigations and many of these studies refer to both seabed habitats and facies. A rock facies was defined by Reading and Levell (1996) as 'a body of rock [including sediment] with specified characteristics' that ideally should be distinctive and formed under certain sedimentary conditions that reflect a particular process or environment. Thus when applied from a contemporary geobiological perspective the terms habitat and facies differ in one critical respect; habitat is defined from the perspective of the organisms that live there, whereas facies also include the geological characteristics of the seafloor and the environmental conditions associated with their formation.

Finally, having discussed the habitats formed by cold-water corals and how these habitats are used by other species, we will return to the habitats occupied by the corals themselves in more detail. As discussed in Chapter 2, cold-water coral habitats are a complex interplay of suitable substrata, oceanography, food supply and many other factors. At the end of the chapter we will discuss how recent work using habitat-suitability modelling is improving our understanding of the factors that characterise cold-water coral habitats and how this can be used to make predictive habitat maps.

5.1.1 Reefs

Cold-water scleractinian coral reef development was described in Chapter 4. Coral recruitment, growth, framework production, sediment trapping and bioerosion all lead to a highly varied structural habitat that may persist for millennia (Fig. 5.1, see also Sections 4.4, p. 119 and 4.5, p. 135). The best-studied cold-water scleractinian coral reefs are those formed by *Lophelia pertusa* in the northeast Atlantic and, among these, perhaps the most extensive are those found on the Norwegian continental shelf (see Case study 5.1). As well as the broad

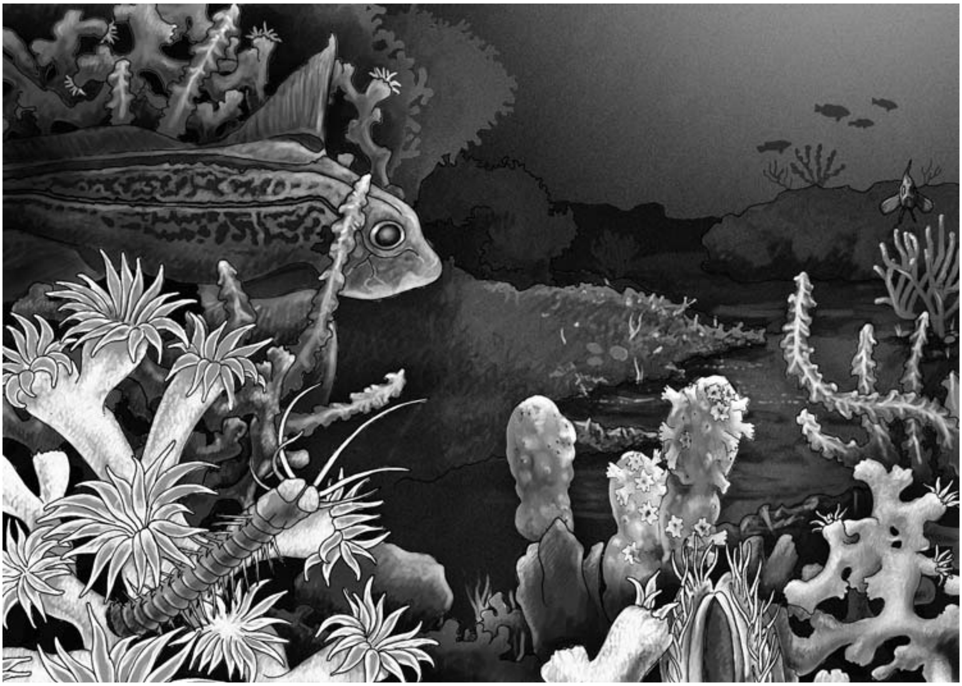


Fig. 5.1. Artist's impression of a *Lophelia pertusa* cold-water coral reef habitat. The foreground shows live *L. pertusa* polyps with a symbiotic polychaete worm (*Eunice norvegica*) emerging from its tube. To the right are gorgonian corals, zoanthids and the large bivalve mollusc *Acesta excavata*. Individual coral reefs can be seen in the background. A rabbitfish (*Chimaera monstrosa*) swims by and several redfish (*Sebastes*) can be seen hovering above the reef structure.

macrohabitat distinctions between live coral, dead coral framework and coral rubble, *L. pertusa* reefs provide an array of microhabitats such as those categorised by Mortensen *et al.* (1995) as: (1) the smooth surface of living coral, (2) the detritus-laden surface of dead coral, (3) the cavities made by boring sponges within the coral skeleton and (4) the free space between coral branches. In other regions of the world other reef framework-forming cold-water corals are found (see Section 2.2.1, p. 25) and similar habitat types are likely to be present although they have yet to be studied in detail. Of these, *Goniocorella dumosa* and *Desmophyllum cristagalli* (= *D. dianthus*) were reported in the Pacific by Squires (1965) forming a large 'coppice' structure 40 m in height and up to 700 m in diameter on the Campbell Plateau, New Zealand. Squires gathered dredge samples from this structure and noted that although the most abundant coral was *G. dumosa*, the pseudocolonial *D. dianthus*, with its robust skeleton, was probably the primary reef framework-constructor. Mullins *et al.* (1981) described dredge hauls from cold-water coral mounds at depths of 1000–1300 m on the

Case Study 5.1 ***Lophelia* reef habitats of the Sula Ridge, Norway**

The *Lophelia* habitats of the Norwegian continental shelf are among the most extensive and most thoroughly studied of any cold-water coral reef system. Some regions of mid-Norway have been the target of detailed seabed mapping for the oil industry and, by assuming that the density of reefs mapped in 1% of the mid-Norwegian shelf are consistent across the area, Mortensen *et al*. (2001) calculated that 6300 individual reef structures covering around 35 km^2 might exist. More recent mapping, notably of the Røst reefs off the Lofoten Islands summarised by Fosså *et al*. (2005), suggests this may be an underestimate. Even though estimates like these are preliminary and must be viewed with caution it is clear that this region is globally significant in terms of cold-water coral habitat. At these high latitudes, reef growth has taken place during the Holocene and the oldest coral material recorded is usually 7000–8000 years old. The *Lophelia* reef structures form characteristic habitats that at their simplest can be thought of as forming three major macrohabitats (Fig. 5.2):

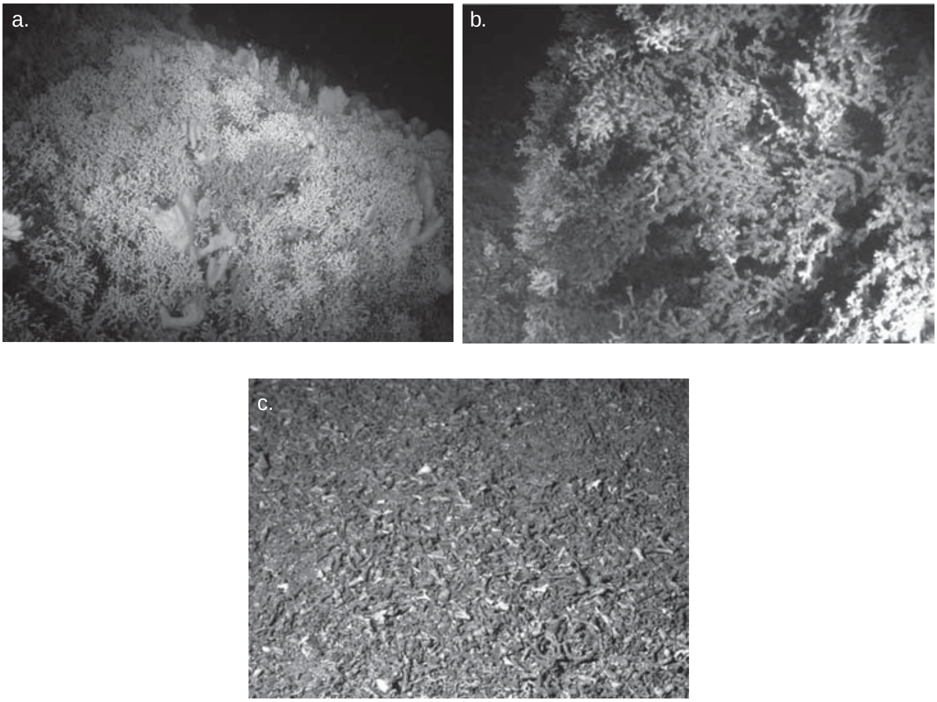


Fig. 5.2. Major macrohabitats in a scleractinian cold-water coral reef. These examples are from *Lophelia pertusa* reefs off Norway. (a) Live coral. (b) Dead coral framework. (c) Coral rubble. Photographs courtesy of JAGO-Team, IFM-GEOMAR.

Case Study 5.1 (cont.)

1. **Living coral**. Found on the summit and upper slopes. Few associated fauna other than symbionts such as the mutualistic polychaete *Eunice norvegica* and parasitic foraminiferan *Hyrrokkin sarcophaga*. Bivalves (e.g. *Delectopecten vitreus*, *Acesta excavata*) may be attached to live coral colonies and mobile animals like echinoids, crustaceans (e.g. *Munidopsis serricornis*) and fish (e.g. *Sebastes viviparus*, *Brosme brosme*) are often present.
2. **Dead coral framework**. This is the most significant structural habitat in terms of associated species diversity. Dead framework is found beneath live coral and on lower slopes of the reef. It is typically characterised by attached, suspension-feeding fauna including numerous sponges, actinians and other coral species (notably gorgonians such as *Paragorgia arborea* and *Primnoa resedaeformis*). Smaller epifauna include bryozoans, hydroids and barnacles. Where sediment becomes trapped in the coral framework niches appear for infaunal species such as polychaete worms.
3. **Coral rubble**. As coral framework is gradually (bio)eroded it accumulates in apron-like deposits at the base of the reef. Here sponges are common and the squat lobster *Munida sarsi* is abundant. Echiuran worms (*Bonellia viridis*) are often seen feeding from their burrows.

lower slope of Little Bahama Bank (western Atlantic) that recovered scleractinians, gorgonians, soft corals, antipatharians and hydroids along with mobile fauna including molluscs, echinoderms and crustaceans. *Solenosmilia variabilis* has been recorded from the South Tasmanian seamounts (Koslow *et al*., 2001) and Heezen Fracture Zone (Zibrowius, 1973) in the South Pacific where it provides extensive cold-water coral reef habitat (Colour plate 20).

5.1.2 Gorgonian forests and coral gardens

Gorgonian cold-water corals can form such large tree-like structures and reach such high densities that fishers in some parts of the world, notably Atlantic Canada, refer to them as ‘trees’ and the areas where they grow as ‘forests’ (Fig. 5.3 and Colour plate 21). The greatest cold-water gorgonian densities recorded so far are from the Aleutian coral ‘gardens’ in the North Pacific (see Case study 5.2) where Stone (2006) reported 0.84 colonies m^{-2}, sometimes up to an order of magnitude greater than gorgonian densities found in Atlantic Canada (0.005–0.048 m^{-2}) by Mortensen and Buhl-Mortensen (2004), off the coast of Norway (0.043–0.069 m^{-2}) by Mortensen *et al*. (1995) and in the Weddell Sea, Antarctica (0.12 m^{-2}) by Orejas *et al*. (2002). Gorgonian assemblages appear to support fewer megafaunal species than scleractinian cold-water coral reefs, probably because the latter provide a greater surface

Fig. 5.3. Artist's impression of a cold-water gorgonian coral forest habitat. Several large colonies of *Paragorgia arborea* are growing attached to exposed rock and boulders on the seabed. The foreground illustrates live polyps of *P. arborea* extended to feed from the water column and a large brittle star entwined round the gorgonian's branches. Several fish are among the corals and a large skate can be seen swimming close to the seabed.

area, volume and diversity of habitat (Metaxas & Davis, 2005). Using submersible observations, Krieger and Wing (2002) reported ten megafaunal taxa with *Primnoa* spp. in the Gulf of Alaska that were using the corals' branches as a place from which to suspension-feed or for protection. They also reported that sea stars, and possibly also nudibranchs, fed on *Primnoa* and that six rockfish (*Sebastes*) species seemed to be associated with the coral colonies. In the Northeast Channel (Atlantic Canada, northwest Atlantic), Buhl-Mortensen and Mortensen (2004a) used suction sampling from a remotely operated vehicle to sample 17 epifaunal crustacean species from *Paragorgia arborea* and *Primnoa resedaeformis* but it was difficult for the authors to tell if these were associated with the corals per se or hydroids that were growing on dead portions of the gorgonian skeleton. When other taxa found with *P. arborea* and *P. resedaeformis* in Atlantic Canada were assessed, nearly 4000 individuals of 114 species were found in just 25 gorgonian samples (Buhl-Mortensen & Mortensen, 2005).

Case Study 5.2 **Aleutian Island coral gardens, northeast Pacific**

The Aleutian Island archipelago is found between the North Pacific Ocean and Bering Sea and extends some 1900 km from the Alaskan Peninsula in North America to the Kamchatka Peninsula in Russia. Submersible surveys have revealed spectacularly beautiful coral habitats prompting observers to refer to them as coral 'gardens' (see Fig. 5.4 and Colour plate 19). At the time of writing 69 coral taxa, excluding the Antipatharia, had been reported from the Aleutian Islands and 25 of these were believed to be endemic (Heifetz *et al.*, 2005). The coral fauna is dominated by gorgonians that occur in great densities with *Plumarella* spp. found at up to 5 colonies m^{-2} in some areas (Stone, 2006). Stylasterids ('hydrocorals') are also an important structural component of the coral habitat but scleractinian corals only occur as solitary species (cup corals). This striking pattern relates to the shallow depth of the aragonite saturation horizon in the North Pacific that appears to prevent significant aragonitic coral framework species from growing to any great extent (Guinotte *et al.*, 2006; Cairns, 2007). The coral gardens develop on exposed bedrock, boulders or cobbles. Although the structural habitat and associated fauna of these coral habitats has yet to be studied in detail, their vertical relief may be several metres

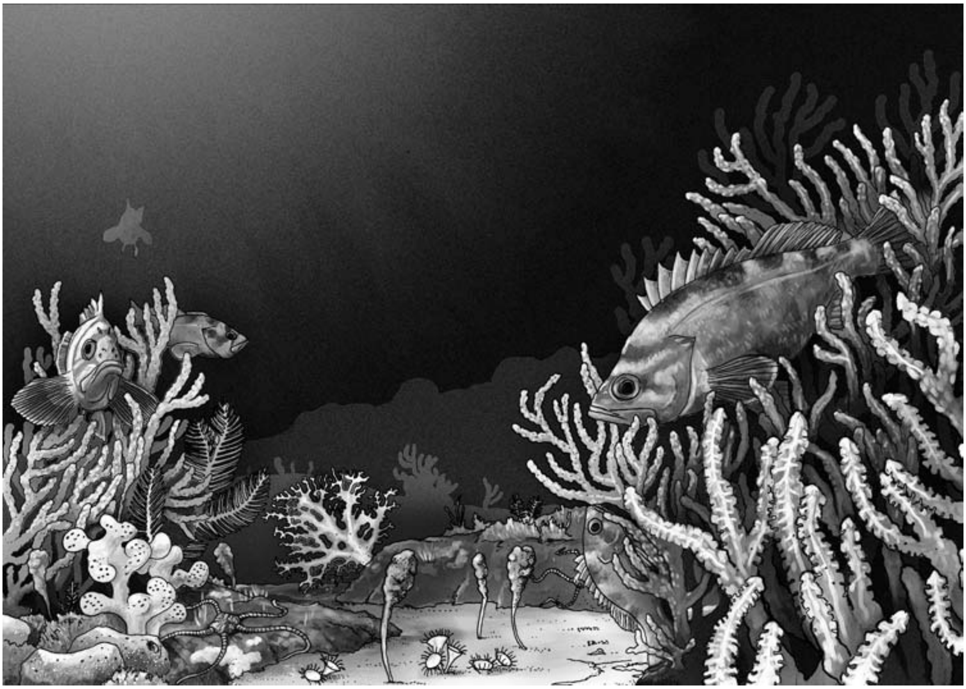


Fig. 5.4. Artist's impression of an Aleutian Island cold-water coral garden habitat. The corals here are dominated by gorgonians and calcitic stylasterids. Many species of rockfish (*Sebastes*) are found among the structurally complex coral habitat.

Case Study 5.2 (cont.)

and they provide elevated feeding positions for other organisms including sponges, sea anemones, holothurians, crinoids and basket stars (Stone, 2006). Heifetz *et al.* (2005) have suggested that the high coral species diversity and endemism found in the Aleutian Island coral gardens is evidence that they may be evolutionary centres for cold-water corals. Interestingly, Lindner *et al.*'s (2008) molecular phylogeny of the stylasterids shows that two stylasterid species found in California (*Stylaster californicus*) and from Washington State to Canada (*Stylantheca petrograpta*) are nested within a clade of deep-water species of *Stylaster* from the Aleutian Islands (*S. verrillii, S. elassotomus, S. cancellatus, S. polyorchis* and *S. campylecus*). This phylogenetic relationship suggests that, at least for some taxa, the Aleutian Islands may indeed have been an evolutionary centre for lineages that subsequently colonised adjacent areas. However, other stylasterid genera found in the Aleutian Islands, such as *Distichopora*, seem to have diversified more extensively in other regions and more work is needed to examine the significance of the Aleutians as an evolutionary centre for cold-water corals.

Thus it has become clear that gorgonian assemblages provide significant habitat for other invertebrate species although their importance for fish populations has been questioned, see Section 5.5 below. But our understanding of the functional ecology of these apparent associations remains very limited. Other than intriguing examples of some, mostly parasitic, symbiotic associations with cold-water gorgonian corals described in Section 5.4.1 below we know very little about how the corals and their associates interact.

5.2 Biodiversity

Biodiversity estimates from cold-water coral habitats have been derived from both visual surveys of the megafauna and by identifying and counting numbers of macro- and meiofaunal species in samples (see Topic box 5.2). Historically, cold-water corals have been sampled by dredging and trawling. For example, Burdon-Jones and Tambs-Lyche (1960) found 300 animal species in dredge hauls from a *Lophelia pertusa* reef near Bergen in Norway and they summarised other early twentieth-century dredging studies. Jensen and Frederiksen (1992) were the first to compare species diversity of *L. pertusa* fauna with that from other corals. They reported Shannon–Wiener diversity indices (H') from Faroese *L. pertusa* framework samples equivalent to or greater than those of communities found with tropical corals in the Gulf of Thailand and Great Barrier Reef. Studies of the fauna found in cold-water coral habitats consistently note the high proportion of suspension and filter feeders such as sponges, bivalve molluscs, brachiopods, cnidarians, bryozoans, and ophiuroid and crinoid echinoderms. However, since the studies to date have used differing collection protocols and varying taxonomic expertise and resolution it is hard or impossible to compare faunal assemblages between studies and determine biogeographic patterns.

5.2.1 Megafauna and macrofauna

A number of authors have compiled lists of species reported with cold-water corals to give an indication of their overall diversity (effectively a simple broad scale ‘gamma’ or regional diversity estimate). Rogers (1999) listed almost 900 species that had been recorded with *Lophelia pertusa* reefs in the northeast Atlantic (excluding the Mediterranean Sea), a total that had increased to just over 1300 following a three-year international research project (Roberts *et al.*, 2006). However, while cold-water coral reefs, such as those formed by *L. pertusa* in the northeast Atlantic, may support many other species, it seems that most of the associated species are facultative. In other words they are drawn from the regional species pool and can be found in other habitats rather than being restricted to the coral habitat in an obligate sense (Burdon-Jones & Tambs-Lyche, 1960; Jensen & Frederiksen, 1992). In the following paragraphs we will focus on

Topic box 5.2 **Size classes**

Benthic ecologists have traditionally categorised animals from the seabed in terms of their size (Mare, 1942; Gage & Tyler, 1991). This rather arbitrary categorisation has developed from the sampling equipment used to either visualise the larger benthic organisms with seabed photography or to separate the smaller infaunal organisms from their sedimentary habitats (see Gage *et al.*, 2002 for discussion).

1. **Megafauna**. Often defined as animals large enough to be seen in seafloor photographs or easily caught in bottom trawls. Further divided into the mobile or *errant* megafauna and the attached or *sessile* megafauna (the latter including cold-water corals).
2. **Macrofauna**. Typically defined as animals retained on a 300–500 μm mesh sieve. Dominated in terms of abundance by the polychaete worms followed by peracarid crustaceans, molluscs, other worms (nemerteans, sipunculids, pogonophorans, priapulids, echiurans, enteropneusts) along with small sponges, pycnogonids, brachiopods, entoprocts and ophiuroids among others.
3. **Meiofauna**. Typically defined as animals retained on a 25 or 32 μm mesh sieve. Dominated by the nematode worms, especially at continental slope depths, with harpacticoid copepods, ostracod crustaceans and foraminiferans.

invertebrate diversity associated with scleractinian cold-water coral habitats, with fish communities discussed later in this chapter.

As one might expect, faunal diversity varies between reef habitats with the fewest species associated with live coral and the most species usually found with dead coral framework (e.g. Jensen & Frederiksen, 1992). But how important is a cold-water coral reef in sustaining high species richness and/or a characteristic suite of species? Few studies have attempted to examine this question by directly comparing the biodiversity and ecological composition between on- and off-reef samples. Henry and Roberts (2007) collected box-core samples from the summits of large coral carbonate mounds in the Porcupine Seabight, northeast Atlantic and compared the fauna with that in box-core samples from off-mound habitat. The on-mound samples were three times as species rich with higher evenness and significantly greater Shannon–Wiener diversity than those off-mound. In total 349 species from 16 phyla were found, of which 313 species were from on-mound samples and 102 species from off-mound samples. Ten of the species found by Henry and Roberts (2007) were new to science. The four species that best discriminated the on- and off-mound habitats are illustrated in Fig. 5.5. In some shallow-water communities one species may dominate the community

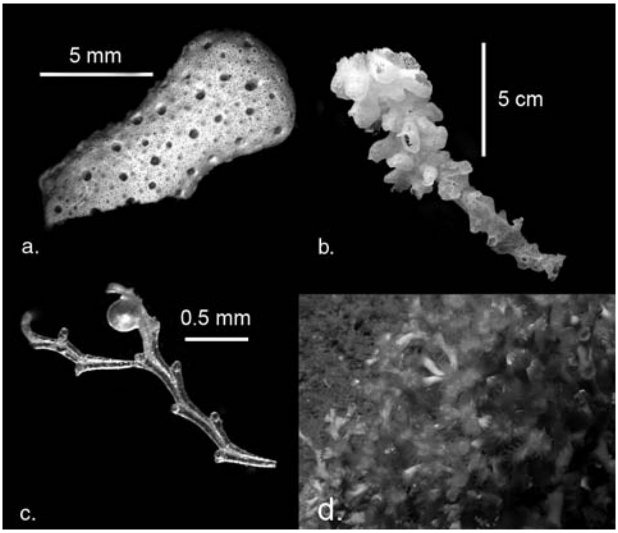


Fig. 5.5. The four species that best discriminated between on- and off-mound habitat from a coral carbonate mound province in the Porcupine Seabight, northeast Atlantic: (a) a broken end branch of the stylasterid coral *Pliobothrus symmetricus* (more frequent off-mound), (b) the hexactinellid sponge *Aphrocallistes bocagei*, (c) a new species of bryozoan *Crisia* nov. sp. and (d) the scleractinian coral *Lophelia pertusa* (all more frequent on-mound). Figure redrawn from Henry and Roberts (2007), with permission of Elsevier.

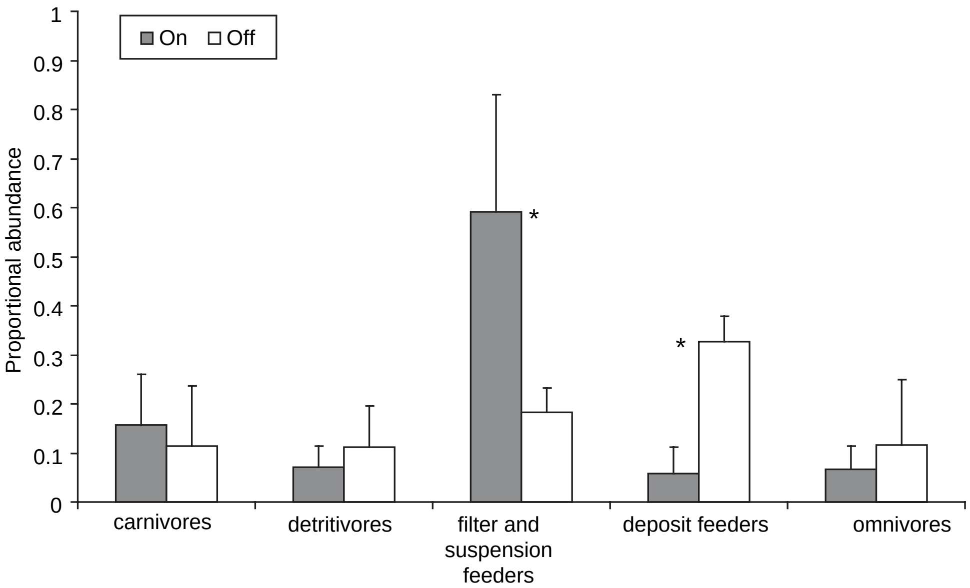


Fig 5.6. Ecological composition of macrobenthos from coral carbonate mounds and surrounding habitats in the Porcupine Seabight, northeast Atlantic. The coral mounds contained more filter and suspension feeders whereas the off-mound habitats supported more deposit feeders. Asterisk indicates statistical significance at $p = 0.05$. Figure reproduced from Henry and Roberts (2007), with permission of Elsevier.

(often forming >80% of the individuals) but in most deep-sea studies dominance of any one species is typically far lower, usually less than 10%, and there are many rare species in the community (Grassle & Maciolek, 1992). This trend was also found in the Porcupine Seabight coral carbonate mounds. There was also evidence that the coral mounds supported a characteristic fauna. For example, 10 out of 12 species of syllid polychaetes were only found on the mounds, probably because this family often lives in symbiosis with corals and sponges (Martin & Britayev, 1998; López *et al.*, 2001; Martin *et al.*, 2002). Finally, when ecological composition of the species was compared, the on-mound samples contained significantly more filter and suspension feeders whereas the off-mound samples contained more deposit feeders (Fig. 5.6). Henry & Roberts (2007) concluded that the high vertical habitat heterogeneity on-mound provided a diverse range of niches over small spatial scales that supported a characteristic ‘reef fauna’. In contrast, off-mound habitats were interpreted as having greater horizontal habitat heterogeneity characterised by varied seabed facies from glacial dropstones to rippled sands. Off-mound a few species that were not present on-mound dominated the community, perhaps because of disturbance from the more abundant off-mound deposit feeders as has been reported in other deep-sea studies (Grassle & Maciolek, 1992).

Thus it is clear that biodiversity can vary considerably across habitats associated with cold-water corals. This suggests that cold-water corals create beta or 'turnover' diversity associated with the variation in habitats they provide and that beta diversity varies within these habitats. Recent work to examine this explicitly indicates that this is likely to be the case in terms of biodiversity of megafauna (Roberts *et al.*, 2008) and macrofauna (L.-A. Henry, personal communication, 2008) associated with cold-water coral reef frameworks. By scoring the presence of megafauna from a large archive of seafloor photographs from Hatton Bank, northeast Atlantic, Roberts *et al.* (2008) showed that some macrohabitat types were notably rich in terms of alpha diversity (coral framework, coral rubble and rock) but others, such as sandy habitats, had higher beta diversity, probably because sandy areas often contained small patches of coral habitat making it a more heterogenous macrohabitat than coral framework. Van Soest *et al.* (2007) found 191 sponge species in their study of samples from coral carbonate mounds southwest of Ireland and compared species richness and abundance at local, between-reef and regional scales. They found the presence of live coral to be a significant predictor of sponge community composition and diversity. Although sponge diversity was greater on dead coral substrata, the association with live coral was interpreted as evidence that environmental conditions that favoured live coral, in terms of food and oxygen flux for example, probably also benefited the sponges. Spatial variation (beta diversity) in sponge community composition was related most strongly to water depth and the presence of live coral (van Soest *et al.*, 2007). The sponge fauna from Mediterranean *L. pertusa* reefs off Cape Santa Maria di Leuca was also strongly structured by depth with two sponge communities present, one at 600–800 m, characterised by *Desmacella inornata* and *Sceptrella insignis*, and another at 800–1100 m, characterised by *Desmacella inornata* and *Hamacantha (Hamacantha) implicans* (Longo *et al.*, 2005).

5.2.2 Meiofauna

On a smaller scale, cold-water coral microhabitats have an important influence on meiofaunal biodiversity. Raes and Vanreusel (2006) identified three distinct microhabitats for nematodes found with cold-water coral reef frameworks in the Porcupine Seabight, northeast Atlantic: dead coral fragments, glass sponge skeletons and the underlying sediment. Each microhabitat contained distinctive (though overlapping) nematode communities with the Epsilonematidae, normally rare in deep-water settings, and Draconematidae families much more abundant on coral than other microhabitats. This is probably because these families are well adapted to feed on the biofilm that develops on exposed dead coral surfaces and can withstand disturbance from erosive current regimes. Both families can move

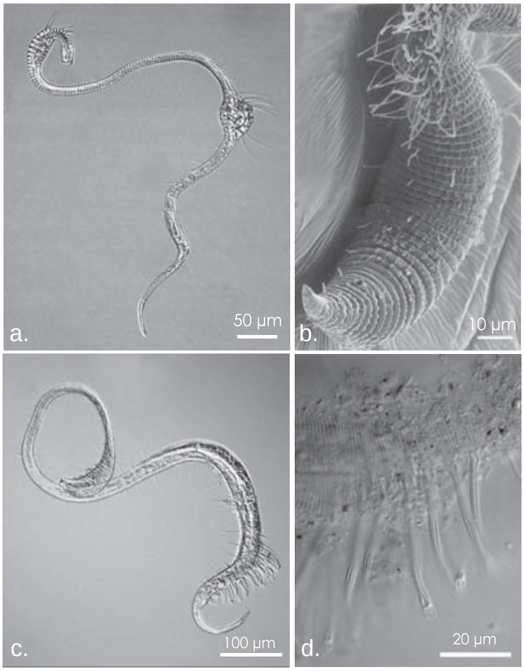


Fig. 5.7. The families Epsilonematidae and Draconematidae best characterise the nematode fauna associated with cold-water corals in the Porcupine Seabight, northeast Atlantic. (a) *Glochinema trispinatum*, (b) *Bathyepsilonema lopheliae* showing ambulatory setae it uses to move across coral surface, (c) *Tenuidraconema* sp. n., (d) *Cygnonema* sp. n. showing posterior adhesion tubes that anchor it to the coral surface. Figure reproduced from Raes and Vanreusel (2005), with permission of Springer.

across the coral surface like inch worms by alternately attaching and releasing their anterior and posterior ends (Fig. 5.7). Thus while emergent, sediment-free structural habitat would generally be considered inhospitable to nematodes, a characteristic nematofauna rare in most continental margin and deep-sea environments is present in cold-water coral reefs and a more typical, rich community of infaunal species is associated with sediment that infills the coral and sponge structures (Raes & Vanreusel, 2006).

5.2.3 *Microbial diversity*

Perhaps the least appreciated aspect of global biodiversity is that found in the protist and microbial communities. Traditionally, microbial diversity has been understood on the basis of which organisms could be cultured to produce unique strains. Since the metagenomic revolution was catalysed by Pace's (1997) study of prokaryotic DNA extracted from environmental samples, it has become possible to identify probable microbial species on the basis of their genetic sequences. It seems that only around 1% of prokaryotic diversity can be cultured in the laboratory (Hugenholtz *et al.*, 1998) but these estimates are continually being revised in the fast-moving field of genomic ecology (López-García & Moreira, 2008). Prokaryotic diversity estimates from sequence data are typically based on the assumption that sequence types with 97–98% similarity to one another form an 'operational taxonomic unit' or OTU.

Such approaches have only been applied to cold-water coral habitats very recently. Penn *et al*. (2006) sampled bamboo and black coral (unfortunately no generic or species identifications were made) from the Gulf of Alaska seamounts and characterised their bacterial communities in comparison to water column and rock biofilm samples. Using clones of amplified 16S rDNA, the rRNA gene sequences formed 19 taxa dominated by *Proteobacteria*, *Firmicutes*, *Bacteriodetes* and *Acidobacteria* and, while the relative proportions of these groups varied between the corals, they were distinct from those found with rock or water samples. There is also preliminary evidence that the cold-water scleractinian *Lophelia pertusa* is associated with a specific microbial community. Yakimov *et al*. (2006) examined the microbial communities with *L. pertusa* from off the Cape Santa Maria di Leuca in the Mediterranean Sea sampled with tangle nets. Again using 16S rDNA sequence analysis, Yakimov *et al*. found distinctive microbial communities on *L. pertusa* that were not present in sediment or water samples taken nearby. The microbial community on *L. pertusa* was dominated by the *Holophaga-Acidobacteria*, *Nitrospira* and α-*Proteobacteria* divisions. Finally, Kellogg (2008) used a submersible equipped with a purpose-built sample storage device to show that *L. pertusa* samples preserved at depth in the Gulf of Mexico showed differences in their microbial communities to samples preserved at the surface. This implies that samples brought back to the surface without being preserved, and samples that are mixed with seabed sediments, may not represent the *in situ* microbial community with the corals.

While there has been a promising start to documenting microbial diversity, nothing is known of the potential functional relationships between these cold-water corals and their microbial communities. Coral-associated microbes could be parasitic agents of disease, particularly when a coral is physiologically stressed (Lesser *et al*., 2007). Indeed, the only study to date giving evidence for a disease affecting a cold-water gorgonian coral, *Eunicella verrucosa*, reported high concentrations of *Vibrio* bacteria from lesions on the coral surface and presented initial evidence that the 'infections' may relate to elevated seawater temperature. The *Vibrio* bacteria produced proteolytic and cytolytic enzymes that could have caused tissue necrosis. However, as in many such studies of coral disease, it proved hard to establish aetiology and seemed that *E. verrucosa* became more susceptible to *Vibrio* bacterial activity when stressed (Hall-Spencer *et al.*, 2007). But apart from disease, microbes could play other, rather more commensal, roles in nutrient acquisition, processing metabolic waste, enhancing skeletal development or by producing biologically active compounds with antibiotic or even antifouling properties. It seems likely that powerful metagenomic techniques, as recently applied to shallow-water marine planktonic microbial communities by the *Sorcerer II* Global Ocean Sampling Expedition (Rusch *et al.*, 2007), have great potential to describe microbial diversity as never before and, when combined with traditional culturing techniques (Giovannoni & Stingl, 2007), metagenomics can unravel potential functional roles of microbial organisms in deep-sea ecosystems.

5.3 Seamounts, endemism and refugia

Endemic species are restricted in their geographic distribution to a particular area or region. Could cold-water coral habitats apparently isolated from one another by large expanses of continental shelf, slope or abyssal sediments function as ecological islands characterised by endemic species? Might they supply species to neighbouring continental slope areas and even play roles as refugia? There is currently little work addressing these questions but there is evidence that some deep-water ecosystems, notably those associated with seamounts, can support high levels of endemism. For example, Richer de Forges *et al.* (2000) found that 29–34% of the fish and invertebrates from seamounts in the southwest Pacific were new to science and potential endemics. Parin *et al.* (1997) reported high fish (44%) and invertebrate (51%) endemism from a compilation of studies from the former Soviet Union of 22 southeast Pacific seamounts. Stocks and Hart (2007) reviewed available endemism estimates from seamounts worldwide and found a great range (0–100%) with an average value of just under 20%. As with the studies of cold-water coral biodiversity summarised above, assessments of seamount endemism are biased geographically, by sampling method and taxonomic resolution so all these estimates need to be interpreted cautiously.

The propensity of species to become endemics will relate strongly to their particular reproductive and dispersal characteristics. Population genetic studies from the southwest Pacific of bamboo corals (Smith *et al.*, 2004) and galatheid crustaceans (Samadi *et al.*, 2006) both showed evidence for genetic connectivity between seamount populations implying larval dispersal between geographically isolated seamounts. However, species with limited dispersal capacities, such as the non-planktotrophic gastropod *Nassaria problematica*, may show population genetic structuring in accordance with geographic distance between populations

(Samadi *et al.*, 2006) indicating the importance of larval dispersal biology in determining the likelihood of endemism developing over evolutionary time.

Thus, although apparently spatially isolated from one another, seamount communities may still be linked genetically. Seamount endemism has been related to isolating mechanisms including the distance to other populations and local hydrographic patterns (such as Taylor columns or tidally rectified anti-cyclonic circulation) that could theoretically trap larvae on a seamount and prevent dispersal and exchange of species (Rogers, 1994; Mullineaux & Mills, 1997). However, seamount hydrography is highly complex and enormously variable (White *et al.*, 2007) and features like Taylor columns should not be assumed to be characteristic of all seamount settings (McClain, 2007). Thus a central issue in understanding seamount biology is whether seamounts function as *islands* (isolated, with high levels of endemism) or *oases* (biologically productive, with high biomass and rich associated fauna). There is general agreement that many seamounts do indeed function as ecological oases where primary and secondary production are locally enhanced and retained, often by upwelling nutrient-rich waters, which in turn support aggregating fish (Morato & Clark, 2007) and rich benthic communities including cold-water corals (Rogers *et al.*, 2007).

Cold-water coral habitats, notably the scleractinian reefs associated with large, long-lived coral carbonate mounds, can form locally enhanced biodiversity centres on the continental shelf and slope. It is possible that in glacial periods, during which high-latitude reef habitat growth stopped, coral carbonate mounds at lower latitudes became refugia for species that spread to higher latitudes when subsequent interglacial climate conditions permitted (see Section 4.4.4, p. 128). Questions of this sort have yet to be examined and only become tractable using ocean basin-scale studies that, given the technical challenges and expense of deep-sea research, will require international co-operation. However, the population genetic approaches outlined in Section 2.6, p. 58 are now being used to follow the phylogeography of shallow-water marine fauna to retrace their invasions and migrations throughout glacial history (e.g. Wares & Cunningham, 2001; Addison & Hart, 2005). Finally, it is worth noting that meta-analysis of shallow-water tropical coral reefs suggests that a high proportion of reef species (corals, fish, snails and lobsters) are restricted to particular centres of endemism that form 'biodiversity hotspots' vulnerable to anthropogenic impact and therefore species extinctions (Roberts *et al.*, 2002). To date we have nothing approaching the density of data on cold-water coral community biodiversity to attempt a comparable analysis but, as discussed in greater detail in Chapter 8, these issues should form a central theme in studies to develop long-term conservation strategies.

5.4 Species interactions

Species may interact in various ways: either competitively, in symbiosis or as predators and prey. Historically, our understanding of such interactions has been largely derived from many years of study and observation of organisms in their natural habitats. But in the deep ocean our ability to observe such interactions is limited to occasional snapshots from remote camera or submersible surveys and these tantalising glimpses have not even begun to give us a true picture of the range and variety of species interactions in cold-water coral habitats. Therefore, our aim in this section is to summarise information gathered from visual surveys, recovered samples and occasional laboratory studies of live animals, and to note that these aspects of cold-water coral ecology are in their infancy.

5.4.1 Symbiosis

Symbiosis was originally defined by de Bary (1879) as the 'living together of differently named organisms'. Such interactions vary on a continuum from parasitism at one extreme to mutualistic symbiosis at the other (Smith & Douglas, 1987; Douglas, 1994), with a relationship that benefits one partner while being neutral to the other referred to as a commensal symbiosis. Invertebrates such as crustaceans and ophiuroids (Colour plates 22, 23) often co-occur with cold-water corals but the nature of the association is rarely known. Buhl-Mortensen and Mortensen (2004c) compiled a list of species apparently associated with cold-water corals and speculated on the nature of the relationship between these 'symbionts' and the coral 'hosts'. Of 980 species recorded with cold-water corals, Buhl-Mortensen and Mortensen characterised 112 species as symbionts with 30 species forming obligate associations. Of the obligate associations roughly half were parasites and half commensals. However, only very few such relationships have been characterised to any extent and care must be taken not to ascribe functional relationships between species that may be found associated coincidently – such as when other suspension-feeding epifaunal species colonise and grow attached to dead portions of coral skeleton.

Cold-water corals can also host parasites. For example the large foraminiferan *Hyrrokkin sarcophaga* can attach to live *Lophelia pertusa* (and occasionally *Madrepora oculata*), dissolve a hole through the skeleton and infest living polyps (Cedhagen, 1994), see Fig. 5.8. *Hyrrokkin sarcophaga* has also been recorded on geodiid sponges and the bivalves *Acesta excavata* and *Delectopecten vitreus*, all species commonly associated with Scandinavian occurrences of *L. pertusa*. A specialised parasitic crustacean species is also known to infest the octocoral *Paragorgia arborea*. This copepod,

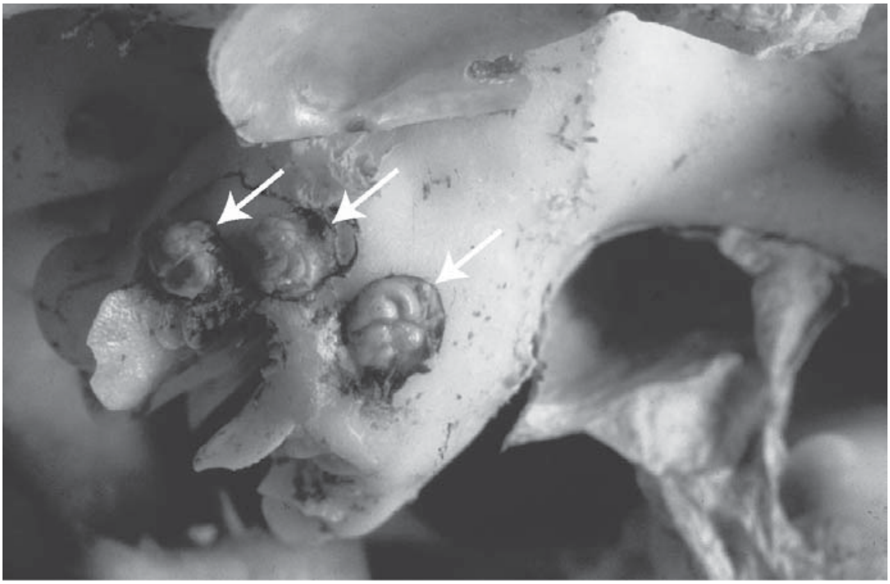


Fig. 5.8. The foraminiferan *Hyrrokkin sarcophaga* (arrowed) attached to a polyp of *Lophelia pertusa*.

Gorgonophilus canadensis, is a member of the Lamippidae, a group of exclusive octocoral parasites that occurs in galls on the coral's branches that typically contain two females, one male and up to eight egg sacs. The adult female copepods live trapped within the galls but it seems that the smaller males, juveniles and larvae might be able to escape through chimney-like structures on each gall (Buhl-Mortensen & Mortensen, 2004b).

A further frequently reported relationship has been noted between stylasterid corals and the prosobranch gastropod mollusc *Pedicularia* (Fig. 5.9). These small molluscs, typically just a few millimetres in length, settle on stylasterids and deposit a layer of calcium carbonate that prevents further coral branch growth beneath, and in outline fit the shape of a snail's shell. This leaves a characteristic trace that can be identified from long-dead stylasterid corals even if the gastropod shell is lost, see Section 6.4.5, p. 204 (Zibrowius & Cairns, 1992). *Pedicularia* gastropods have been found with stylasterids in the northeast Atlantic and Mediterranean (Zibrowius & Cairns, 1992) as well as shallow-water stylasterids from the Indo-West Pacific (Goud & Hoeksema, 2001). It is not clear whether the snails predate on the coral or are commensals that graze coral mucus with no discernable effects on the coral host. Other gastropods have been noted as predators on cold-water corals such as *Calliostoma torrei*, which was reported to be apparently grazing on the bamboo coral *Keratoisis ornata* at 843 m depth in the western Atlantic off Florida (Harasewych & Sedberry, 2006).

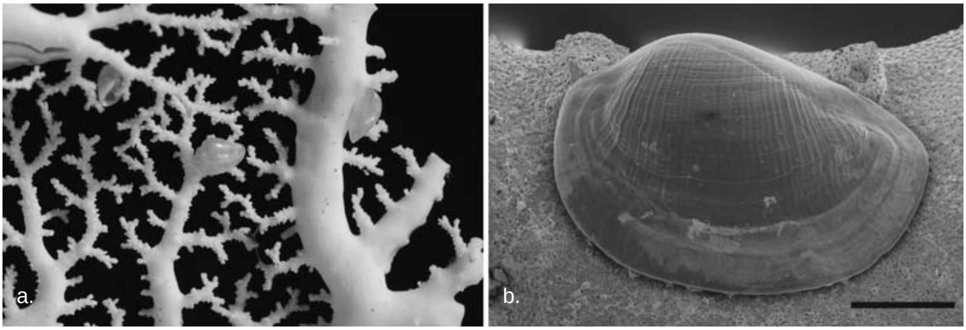


Fig. 5.9. Prosobranch gastropods (genus *Pedicularia*) occur in symbiosis with several stylasterid coral species with their shells forming a close fit to the coral branch where they occur. (a) Several *Pedicularia sicula* on the stylasterid coral *Errina dabneyi* from the Azores (Southern Faial Channel, 490 m depth). (b) Scanning electron micrograph of *P. sicula* on the coral's branch. Scale bar 1 mm. Images courtesy of M. Wisshak.

One of the better characterised symbioses found with cold-water corals is that between the large polychaete worm *Eunice norvegica* and several species of scleractinian and stylasterid coral. These worms secrete a delicate parchment-like tube that becomes calcified by *Lophelia pertusa*, *Madrepora oculata* and *Solenosmilia variabilis*, species that frequently contain live *E. norvegica* (Fig. 5.10). Given its ubiquitous occurrence and the way calcified worm tubes appear to strengthen the coral framework it seems this symbiosis is particularly significant. So far our understanding of this interaction comes from aquarium observations of live *E. norvegica* with the corals *L. pertusa* or *M. oculata*. These have shown that *E. norvegica* appears to form a non-obligate mutualistic association sometimes stealing food from coral polyps but also removing sediment particles (Mortensen, 2001). In a subsequent study using time-lapse video with infra-red illumination to observe polychaete behaviour, Roberts (2005) repeatedly observed the polychaete moving *M. oculata* coral fragments and aggregating them. This implies that in addition to the coral's own (autogenic) ecological engineering (*sensu* Jones *et al*., 1994) via reef framework production, the polychaete symbionts may function as allogenic engineers by aggregating coral fragments and enhancing reef patch development (Fig. 5.11).

As outlined above, a number of these symbiotic associations leave traces, particularly on scleractinian coral skeletons, that can be seen in the fossil record. Among the most prominent of these trace fossils are the boring patterns left by bioeroders in scleractinian coral skeletons. Recent work using three-dimensional x-ray visualisation techniques has shown how boring sponges can spread from dead portions of *Lophelia pertusa* to infest living polyps and dramatically alter

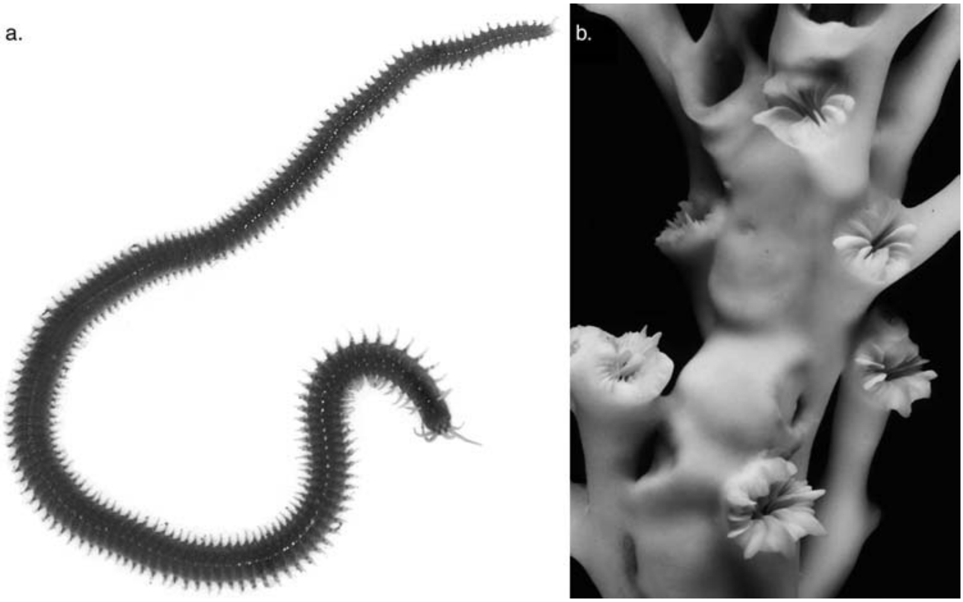


Fig. 5.10. The polychaete worm *Eunice norvegica* (a) forms a significant symbiosis with several reef framework-forming scleractinian corals including *Lophelia pertusa* (b), which calcifies over its parchment tubes adding strength to the coral skeleton and providing protection to the worm.

their morphology (Beuck *et al.*, 2007). These interactions, along with others that help explain palaeontological variability, are described in Section 6.3.2, p. 194.

5.5 Fish assemblages

A characteristic of tropical coral reefs is the staggering diversity of fish species they support. This, plus their accessibility and attractiveness, has in turn spawned a large literature examining the biology and ecology of tropical coral reef fishes, the reasons behind their diversity and their habitat associations (see Sale, 1991, 2002). Cold-water coral habitats are associated with dramatically fewer fish species than their shallow, tropical counterparts, tracking a general decline in overall numbers of fish species with increasing depth. But to what extent is cold-water coral habitat important for local fish populations? Might corals provide shelter, spawning grounds or sites where juvenile fishes develop? These issues have come to the fore in recent years, particularly since the dramatic evidence of bottom trawl fishery damage to cold-water coral habitats came to light and because, in some nations, if coral habitat was proven 'essential' to fish populations, then legislative mechanisms designed for fishery conservation could be used to promote their conservation (see Section 8.1.1, p. 237).

Fig. 5.11. Reef aggregating behaviour of *Eunice norvegica* with *Madrepora oculata* collected from a coral carbonate mound in the Porcupine Seabight, northeast Atlantic (820 m depth). These video frame-grabs taken under infra-red light show the worm (centre right) moving a coral fragment 4 cm across the glass base of an aquarium tank. The transplantation took just over a minute. Time-lapse sequence runs from left to right. Image reproduced from Roberts (2005), with permission of Cambridge University Press.

As with other aspects of our understanding of cold-water coral habitats, our appreciation of their fish fauna and habitat affinities is greatly limited by a lack of data. Regional knowledge of deep-water fish occurrence is largely based upon historic trawling surveys (e.g. Gordon, 2001) that integrate species distributions over the distance covered by the trawl so limiting any subsequent spatial analysis. Where site-specific information is available, for instance from targeted submersible or ROV surveys, we cannot be sure what effect a brightly lit, often acoustically noisy, vehicle might have on a mobile fish fauna. Some species are attracted to the submersible and others are repelled. For instance some species, such as saithe (*Pollachius virens*) and rabbitfish (*Chimaera monstrosa*), were attracted to feed on zooplankton aggregated by the lights during submersible surveys of *L. pertusa* reefs in Norway, whereas poor cod (*Trisopterus minutus*) apparently avoided the submersible and redfish (*Sebastes*) seemed unaffected (Costello *et al*., 2005). Similar issues were reported from submersible fish census surveys in the Gulf of Mexico where some species appeared to follow the submersible during belt transect surveys (Sulak *et al*., 2007). On the New England seamounts (northwest Atlantic) the false boarfish (*Neocyttus helgae*) was even provoked into territorial behaviour, raising its dorsal fin spines and attempting to bite the ROV (Moore *et al*., 2008). But despite these artefacts, most deep-water fish researchers believe that direct observation methods provide an essential perspective on deep-water fish assemblages.

A number of submersible and ROV surveys of cold-water coral areas have noted that fishes were associated with coral habitat. Krieger and Wing (2002) reported six rockfish (*Sebastes*) species with gorgonians (*Primnoa*) in the Gulf of Alaska. The redfish *Sebastes viviparus* and *S. marinus* are frequently reported with Scandinavian reefs of *Lophelia pertusa* (Colour plates 6, 17) where experimental long-line fishing recovered greater *S. marinus* catches from lines set in coral compared with adjacent habitats (Husebø *et al*., 2002), and visual observations showed high densities of gravid redfish in *L. pertusa* reefs in springtime surveys (Fosså *et al*., 2000, 2002; Costello *et al*., 2005). Costello *et al*. (2005) recorded fish observations from a compilation of video and still photographic studies of *L. pertusa* reefs in the northeast Atlantic and concluded that while the reefs did not support distinct assemblages, over 90% of fish species and 80% of individuals were associated with reef habitat.

A subsequent, larger scale analysis of fishes associated with *L. pertusa* mounds on the Blake Plateau, southeast United States, indicated that cold-water coral reefs not only supported more fish species but also a characteristic assemblage of species compared with off-reef areas. Ross and Quattrini (2007) made 65 dives over a six-year period using the Johnson-Sea-Link manned submersibles (Colour plate 4) to coral and adjacent habitats. As well as these visual surveys, they collected fishes with the submersible and made otter trawls in off-reef and transitional reef habitats to help identify the fish species recorded visually. They found 99 fish species on and near coral habitat between 356 m and 910 m depth with prime reef habitat best characterised by the alfonsino *Beryx decadactylus*, the blackbelly rosefish *Helicolenus dactylopterus*, the gadiform *Laemonema melanurum* and the roughtip grenadier *Nezumia sclerorhynchus* (Colour plate 24). Interestingly, some species seemed specifically associated with coral habitat (e.g. *Anthias woodsi*, *B. decadactylus*, *Conger oceanicus* and *Dysommina rugosa*), whereas others were more associated with off-reef habitat (e.g. *Chlorophthalmus agassizi*, *Benthobatis marcida*, *Fenestraja plutonia* and *Phycis chesteri*). Some of the reef-associated species, such as *B. decadactylus*, were mostly observed swimming above the reef whereas others, like the large eel *C. oceanicus*, were

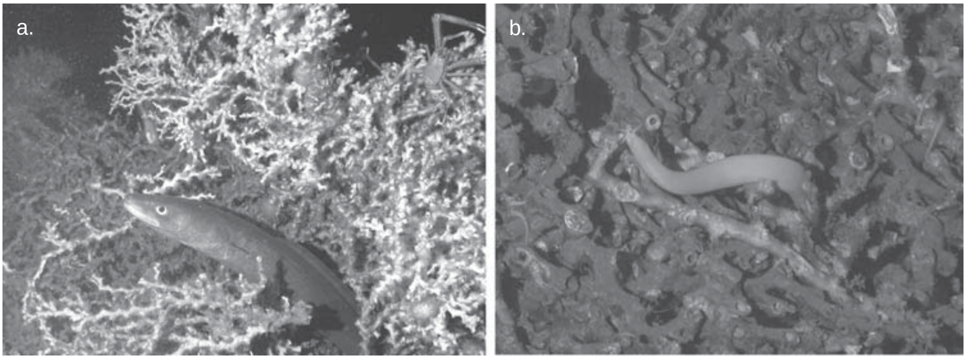


Fig. 5.12. Two examples of fish species that were closely associated with *Lophelia pertusa* coral framework on the Blake Plateau, southeast United States: (a) *Conger oceanicus* (see Ross & Quattrini, 2007); (b) *Eptatretus lopheliae* (see Fernholm & Quattrini, 2008). Photographs courtesy of S. Ross and collaborators.

closely associated with the reef structure and either their heads or tails were often seen projecting from coral frameworks (Fig. 5.12). Whereas most of the off-reef fish species were already known from the study area, almost a fifth of the reef-associated fishes were previously unknown from the area or were considered rare. Indeed one of the closely associated fishes was found to be a new species of hagfish (Myxinidae) subsequently described as *Eptatretus lopheliae* (Fernholm & Quattrini, 2008). Over 90% of the observations of this new species showed it within *L. pertusa* reef structure, which is unusual for hagfish as they are generally associated with soft substrata, although other newly described species have also been related to hard substrata associated with seamounts (*E. eos*, Fernholm, 1991) and hydrothermal vents (*E. lakeside*, Møller & Jones, 2007).

While there is gathering, albeit somewhat circumstantial, evidence that the large biogenic reef structures formed by *L. pertusa* may support characteristic fish assemblages most of the species are also found in other habitats and it is not clear that the coral habitat is *essential* to fish life histories. Are the fishes found in cold-water coral habitats simply aggregating around structural habitat, much as fish species aggregate around rocky reefs or even artificial reefs like shipwrecks and oil platforms? Auster (2005) compared fish assemblages between coral and non-coral habitats in the Gulf of Maine, northwest Atlantic. The coral habitats in the study site were formed by octocorals (primarily *Paragorgia*, *Paramuricea*, *Primnoa*, Plexaurid sp.), which varied from one study site with dense coral cover to others with sparse coral or epifaunal cover. Other sites had structural habitat in the form of boulders and outcropping rock with some characterised by rich epifauna while others were bare. Auster found that fish assemblages in dense coral and epifaunal habitats were most similar to one another; with the next most similar fish assemblage found with habitat formed by outcropping rock, boulders and cobbles. These habitats were all characterised by large numbers of Acadian redfish (*Sebastes fasciatus*). When Auster compared densities of redfish between habitats structured by octocorals and those structured by boulders and outcropping rock he found little evidence for any difference. Therefore Auster concluded that while cold-water corals may influence fish distribution and abundance, they do not appear to support unique fish communities of any greater diversity or density compared with other structural habitats (including other biogenic habitats such as sponges).

On balance, however, while many methodological difficulties associated with gathering data on deep-water fish density and habitat use need to be addressed, there are preliminary indications of fish species that make specific use of coral habitat, albeit probably facultatively. For example, Sulak *et al*. (2007) found that *Grammicolepis brachiusculus* (thorny tinselfish), a microcarnivore apparently well adapted to prey on small crustaceans in reef structure, was tightly associated with *L. pertusa* reef framework in the northern Gulf of Mexico. *Neocyttus helgae* (false boarfish), a member of the same order (Zeiformes or dories) as *G. brachiusculus*, has also been recorded with *L. pertusa* reefs in the northeast Atlantic (Costello *et al*., 2005), Porcupine Seabight (Foubert *et al*., 2005) and with *Paragorgia* colonies on the New England seamounts (Auster *et al*., 2005). Auster *et al*. found that *N. helgae* behaved differently from other seamount fish in that it seemed to use rock and coral structure as a flow refuge from which to feed. Auster *et al*. also observed *N. helgae* picking at coral and sponges, perhaps predating on the corals' polyps or taking prey species associated with them.

Debate on the importance of cold-water coral habitat to fish populations will continue as more studies examine this question in a variety of coral habitats. It seems likely that the degree of any association will vary depending on the coral habitat and there is emerging evidence that some cold-water coral habitats, notably long-lived *L. pertusa* reefs, may concentrate food resources to help sustain distinctive reef fish communities (Ross & Quattrini, 2007; Sulak *et al*., 2007). But as discussed, our observations to date are at best brief glimpses in time and space. It will be necessary to consider coral–fish associations both spatially and temporally (including seasonality) to develop a proper picture of the ecological significance of cold-water corals for fish populations (Auster, 2007).

Having considered the importance of cold-water coral habitat for other species, from microbes to megafauna, we now return to the characteristics of the environment that allow cold-water coral habitats to develop and flourish. The next section develops work described in Section 2.3, p. 43, to summarise how new approaches of habitat suitability modelling have advanced our understanding of the ecological niches occupied by cold-water corals and allowed the first predictive habitat maps to be produced.

5.6 Predictive mapping

The distributions of cold-water coral species are likely to be regionally biased to a greater or lesser extent by the level of deep-water research and exploration. Many cold-water scleractinian coral records come from the North Atlantic, with its long history of deep-ocean research and fishing activity. However, it seems that the North Atlantic, which has a particularly deep aragonite saturation horizon, may be particularly suitable for aragonitic cold-water corals (see Section 2.4, p. 52). It also seems that many other regions of the world's oceans could provide suitable habitat for cold-water corals but they have yet to be explored. As evident from the global distribution of major reef framework-forming cold-water corals there are major gaps in the distribution with no records, such as the Indian Ocean. It would therefore be of great interest to try to estimate or predict where cold-water coral habitats would be likely to occur, especially to see whether unexplored oceans might provide suitable conditions. Such information could also be useful to help design marine reserves to protect vulnerable deep-water ecosystems from damaging anthropogenic activities (see Section 8.2.1, p. 255). But conventionally such a model would need to be developed using data both on where a species was known to occur and known not to occur, in other words by using data on *absence* as well as presence. Historical records of habitat-forming cold-water corals are restricted to notes on where a species was found to occur. In many instances the majority of such data compilations relate back to records from deep-water fishing activity, such as for *L. pertusa* in the northeast Atlantic (Roberts *et al.*, 2003) and for gorgonian assemblages in the northwest Atlantic (Gass & Willison, 2005). Comparable absence datasets of sampling events that did not gather corals do not exist. Given this, and the overall sparse and patchy nature of any deep-water species' distributional record, a technique capable of predicting species occurrence based only on presence data is required.

Ecological niche factor analysis (ENFA) is a technique, similar to principal component analysis, that has been specifically developed to work with presence-only datasets (Hirzel *et al.*, 2002) and its first use with marine species was to predict habitat for cold-water gorgonian corals in the northwest Atlantic (Leverette & Metaxas, 2005). The basic principle of ENFA combines data on the known distribution of a species with a set of environmental data to determine the characteristics of the species' niche. By then examining where suitable niches are predicted to occur, ENFA can be used to see where suitable habitat for the species in question is likely to be found, and by inference where that species could occur. The freely available 'Biomapper' software then allows the output from ENFA to be converted into habitat suitability maps (Hirzel *et al.*, 2002). To run this analysis a series of 'ecogeographical variables' are needed from the area where the species occurs. For cold-water corals these might include factors such as depth of occurrence, seabed slope angle, current speed, temperature and primary productivity. An ecological niche was elaborated by Hutchinson (1957) as a 'hypervolume' encapsulating the environmental conditions within which a species exists and maintains a viable population. The concept of an ecological niche used in ENFA follows this logic in that the eco-geographical variables are used to derive a geographical space in which the species in question is likely to occur (Hirzel *et al.*, 2002).

Thus ENFA computes factors that explain the ecological distribution of the species. The first factor describes how much the species optimum in any eco-geographical variable differs from the global mean of that variable. Known as the 'marginality' of the species' niche this factor usually ranges between zero and one, with low values indicating that a species is found in conditions widespread in the global range and high values indicating that a species is found in conditions that are rare. The remaining 'specialisation' factors explain how restricted the species' niche is in relation to the area being studied with higher values indicating that the species is restricted to a narrow range of conditions (Hirzel *et al.*, 2002). The concepts of marginality and specialisation are illustrated in Fig. 5.13. A final output of ENFA is an index of species 'tolerance'. Tolerance values are the

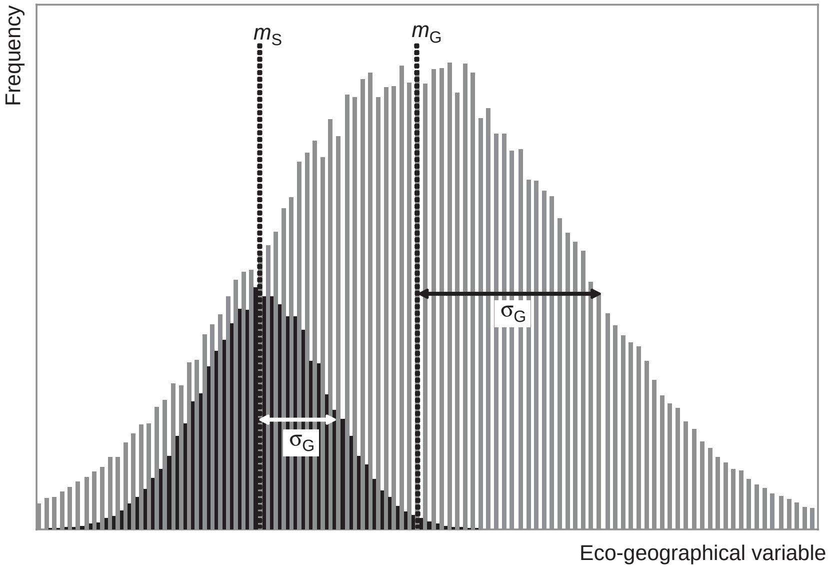


Fig. 5.13. Ecological niche factor analysis (ENFA) calculates two factors. The first, marginality, is the absolute difference between the global mean (m_G) and species mean (m_S) divided by 1.96 standard deviations (σ_G) of the global distribution. The second, specialisation, is the ratio of the standard deviation of the global distribution (σ_G) to that of the focal species (σ_S) (Hirzel *et al.*, 2002). Figure redrawn from Hirzel *et al.* (2002), with permission of the Ecological Society of America.

inverse of specialisation and indicate how tolerant a species may be of inhabiting a wide range of conditions.

An ENFA is visually represented using a 'habitat suitability' map that takes the combined analysis of eco-geographical variables and plots the likely habitat suitability for a species' occurrence. The first habitat suitability maps for cold-water corals were generated for the gorgonians *Paragorgia arborea* and *Primnoa resedaeformis* in Atlantic Canada, northwest Atlantic (Leverette & Metaxas, 2005). In this study Leverette and Metaxas used a 9 × 9 km grid and generated eco-geographical variables from data on temperature, surface chlorophyll *a*, substratum, current speed, bathymetry and slope (which they derived from bathymetry). An ENFA model can be tested by seeing how well a set-aside subset of the presence dataset used to generate the model aligns when compared to the habitat suitability model. This is done in two ways (Hirzel *et al*., 2004). Firstly, the absolute validation index (AVI) calculates what proportion of the set-aside validation data points coincides with a habitat suitability index of greater than 50%, so a higher AVI indicates a model with a good fit to the data. Secondly, the contrast validation index (CVI) is the difference between the AVI of the model and an AVI produced for a randomly distributed species and, once again, higher CVI values indicate a more accurate model. Leverette and Metaxas (2005) found that the best combination of AVI and CVI for *Paragorgia arborea* derived from a model including slope, average temperatures, current speeds, maximum chlorophyll *a* and substratum. In a subsequent, extended analysis Bryan and Metaxas (2007) used a higher resolution grid and included other Paragorgiidae and Primnoidae species. The habitat suitability maps generated showed that for the Paragorgiidae the most suitable conditions were predicted to occur in a narrow band along the shelf break (Fig. 5.14a). In contrast, the best model for the Primnoidae related to conditions that were similar to the average conditions across the study area and the map for this species predicts suitable habitat across the continental shelf and shelf break (Fig. 5.14b). This pattern was mirrored in the marginality and tolerance values: both *Paragorgia arborea* and *Primnoa resedaeformis* had similar marginality scores, implying they would co-occur, but the higher tolerance score of *P. resedaeformis* underlines that this species is likely to tolerate a wider range of conditions than *P. arborea* (Leverette & Metaxas, 2005).

Recently, two further studies have used ENFA to assess habitat suitability for scleractinian cold-water corals. The first by Clark *et al*. (2006) used a database of scleractinian coral records associated with seamounts, but shallower than 2500 m depth, and environmental data expressed at 500 m depth intervals. Clark *et al*. modelled habitat suitability for these depth zones across the global oceans without specifically including seamount locations so as to overcome difficulties with aligning the known location of coral records with the inferred seamount

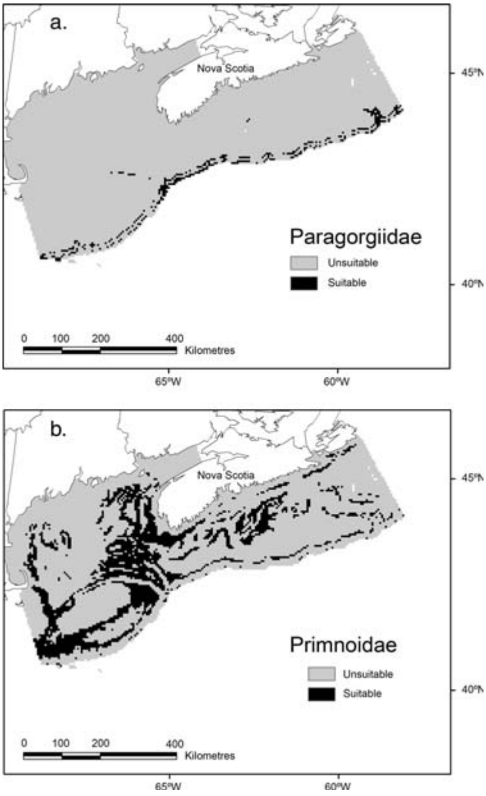


Fig. 5.14. Habitat suitability maps for (a) Paragorgiidae and (b) Primnoidae species in the northwest Atlantic off Nova Scotia (Canada). Maps were generated using ecological niche factor analysis (ENFA) with a combination of environmental data including depth, temperature, slope and surface chlorophyll concentration. Figures reproduced from Bryan and Metaxas (2007), with permission of Inter-Research.

locations they used (based on Kitchingman & Lai, 2004). The assumption is that if a suitable seamount structure were present in areas predicted to provide an otherwise suitable niche then scleractinian cold-water corals could be expected to occur. This approach showed that large parts of the surface ocean (0–250 m depth) in the southern North Atlantic, South Atlantic, Pacific and southern Indian Ocean could provide suitable seamount coral habitat. But at greater depths a more complex story developed. Between 250 m and 750 m depth bands of suitable habitat become apparent in the southern North Atlantic, the South Atlantic, the South Pacific and southern Indian Ocean. At these depths the model predicted an almost continuous band of suitable habitat around 40°S but the North Pacific and northern Indian Ocean appear unsuitable. While depths of 250–750 m were predicted to provide the most suitable scleractinian coral habitat globally, suitable habitat was predicted down to depths of 2500 m in the North Atlantic (Clark *et al*., 2006). The lack of suitable habitat in the North Pacific compared to the North Atlantic Ocean can be explained by the shallow aragonite saturation horizon in the Pacific compared to Atlantic, see Section 2.4, p. 52 (Guinotte *et al*., 2006). Clark *et al*.'s analysis produced a high marginality value (0.918) showing that scleractinian coral habitat was rare compared to the global average, and a specialisation value (1.369) indicating the corals occupied a relatively narrow environmental niche. The most important factors in predicting suitable habitat were dissolved oxygen, dissolved inorganic carbon and aragonite saturation state. On a global scale this indicates that scleractinian cold-water corals are unlikely to be found in water masses of low aragonite saturation state or within oxygen minimum zones.

The second study to predict suitable habitat for scleractinian cold-water corals focused on the dominant reef framework-forming species *Lophelia pertusa* (Davies *et al*., 2008). This study operated on two spatial scales, a global analysis (1° cell size) and a northeast Atlantic regional analysis (0.25° cell size). Eco-geographical variables included aspects of seawater chemistry (e.g. alkalinity, aragonite saturation state, nutrients), surface productivity, depth, slope, current speed, temperature as well as data on potentially important controlling geological factors (e.g. distance to iceberg ploughmarks and hydrocarbon seeps). The ENFA for *L. pertusa* revealed some interesting trends about the modelled niche for this species and highlighted several limitations with the resolution of data used to derive the eco-geographical variables. For example, while the model showed *L. pertusa* was likely to be associated with intermediate depths, productive waters and higher than average current speeds it also predicted occurrences at temperatures well outside this species' known tolerance. This was because the resolution of grid used to derive eco-geographical variables was sometimes too coarse to replicate areas where temperature changed rapidly across small spatial scales, such as in the Faroe–Shetland Channel where a thermocline at approximately 500 m depth divides warmer 5–8°C surface North Atlantic waters from near-freezing Arctic water masses beneath, where no *L. pertusa* occurrences have been found (Roberts *et al*., 2003).

The habitat suitability maps generated by Davies *et al*. (2008), see Fig. 5.15, showed that on a global scale the North Atlantic provides particularly suitable habitat whereas the North Pacific, with its shallow aragonite saturation horizon, does not, see Section 2.4, p. 52 (Guinotte *et al*., 2006). The analysis indicated that *L. pertusa* occurred preferentially in oxygen levels of 6 $\mathrm{ml\,l^{-1}}$ with minimum values on the regional northeast Atlantic scale of 4.3 $\mathrm{ml\,l^{-1}}$. Interestingly, recent work on the respiratory physiology of this coral supports this prediction since *L. pertusa* cannot maintain its respiration rate below 3.3 $\mathrm{ml\,l^{-1}}$ oxygen, see Section

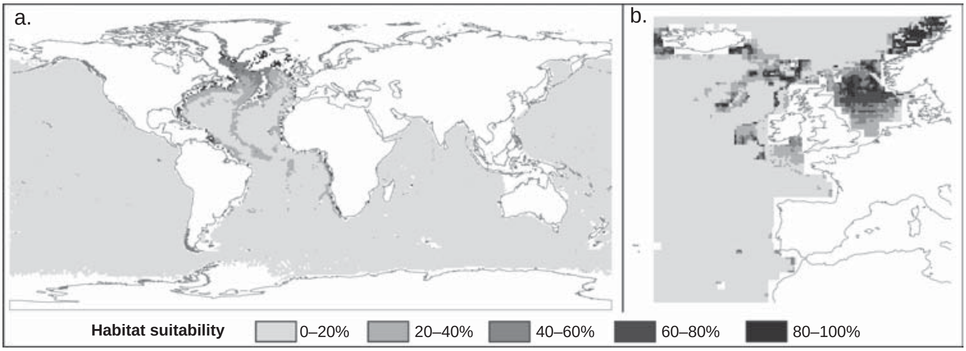


Fig. 5.15. Habitat suitability maps for *Lophelia pertusa* on (a) global and (b) regional northeast Atlantic scales. High percentages indicate more suitable habitat. Gaps correspond to areas excluded from the analysis where there were insufficient environmental data to generate eco-geographical variables. Figure redrawn from Davies *et al*. (2008), with permission of Elsevier.

3.5.1, p. 96 (Dodds *et al*., 2007). The niche factor analysis for *L. pertusa* also showed that this species was associated with below-average nitrate, phosphate and silicate concentrations, particularly on a global scale, indicating this might be a fruitful avenue for future research on environmental controls on cold-water scleractinians. Marginality values for *L. pertusa* showed that it was found in areas very different from both the global (marginality = 3.2) and regional (marginality = 1.5) means, as was the case with cold-water scleractinians associated with seamounts (Clark *et al*., 2006).

Predictive modelling of this sort has considerable potential to improve our understanding of the ecological niche occupied by different cold-water corals, although its utility in predicting where suitable habitat occurs is severely limited by the resolution of available environmental datasets. This was brought into sharp focus by the recent study of Bryan and Metaxas (2007), which used ENFA to predict suitable deep-water gorgonian habitat on the continental margins of the northwest Atlantic (see Fig. 5.14) and northeast Pacific Oceans, extending the pioneering study of Leverette and Metaxas (2005) described above. The habitat suitability maps generated by Bryan and Metaxas (2007) were restricted to regions of 'suitable' and 'unsuitable' habitat because of the coarse resolution of the environmental data used to generate eco-geographical variables. Echoing the findings of their 2005 study, Bryan and Metaxas found that suitable habitat for Paragorgiidae corals in the northwest Atlantic was restricted to the continental shelf break whereas Primnoidae habitat was distributed across the continental shelf. However, the habitat suitability maps in the northeast Pacific showed suitable habitat for both families to be very spatially limited prompting Etnoyer and Morgan (2007) to raise the concern that such maps could be misleading and might lead to areas of potentially important habitat for deep-water gorgonians remaining unprotected from anthropogenic impact, notably bottom trawling (see Section 8.1.1, p. 237). There is clearly an urgent need not just to gather new environmental data but to re-appraise and model existing data to improve its spatial resolution and its utility for future deep-water predictive habitat modelling for cold-water corals (Metaxas & Bryan, 2007; Davies *et al.*, 2008).

We now leave present-day discussions of the ecology of cold-water coral habitats to consider their significance in the fossil record, both in terms of the history of their development from a palaeontological perspective and in terms of the palaeoecological record.

6

Palaeontology

> *Richly coralliferous biostromal and biohermal limestones are widely regarded as indicators of a clear, warm, shallow-water depositional environment. If in such rocks coral organisms are associated with a rich bryozoan, brachiopod, molluscan, and echinoderm fauna, this conclusion will by most geologists be considered to approach the certainty of an observational fact. . . . this conclusion is not necessarily valid.*
>
> Cold- and deep-water coral banks.
> Curt Teichert (1958)

This chapter brings a new dimension to the understanding of cold-water coral habitats by considering cold-water corals from the temporal perspective of the fossil record. We will focus on the calcified Scleractinia as their stony skeletons are widely preserved in ancient rocks. The early evolution and phylogeny of Scleractinia have been studied by comparing morphological characteristics of extant and extinct corals, their skeletal ultrastructure and, recently, by using molecular phylogenetics (see Section 2.5, p. 52). However, none of these approaches have so far provided a unified theory for the origin of the Scleractinia. The present-day coral reef ecosystem, both in shallow and deep waters, is a geologically young achievement and its fossil record is a fascinating story of extinctions and radiations mirroring dramatic changes in the Earth's climatic history. This chapter sheds light on the fossil record of the main habitat-forming cold-water coral genera *Lophelia, Madrepora, Goniocorella, Oculina* and *Enallopsammia* and it describes fossilisation processes that control the quality of preservation in this record.

6.1 Triassic dawn

What does the fossil record of the Scleractinia tell us about their ancestry? Compared to other calcified metazoan orders that arose in the Palaeozoic, the

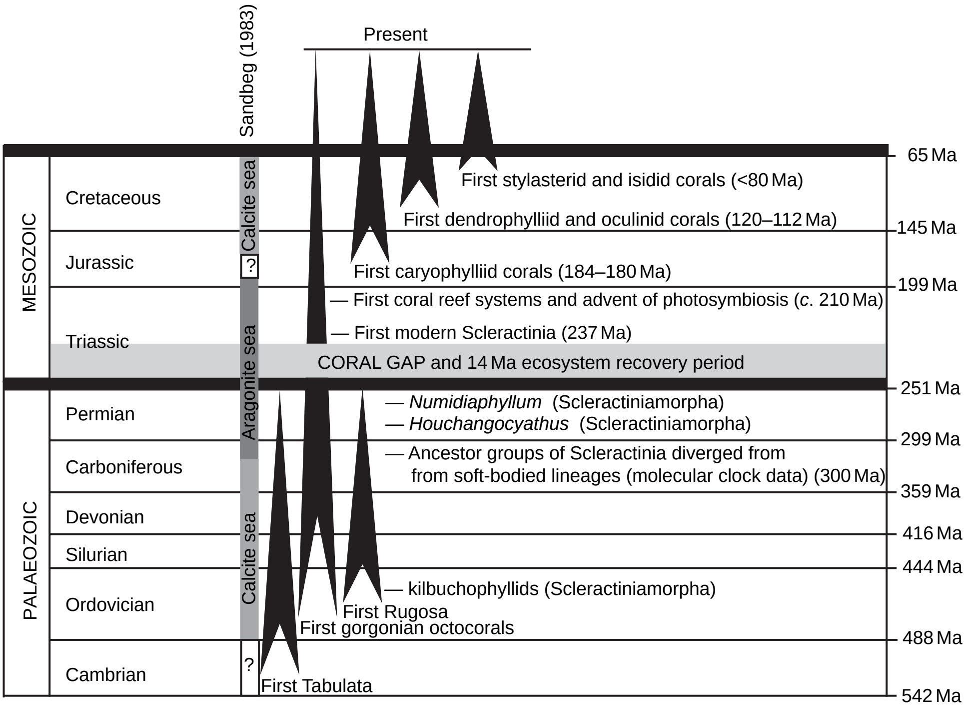


Fig. 6.1. Temporal evolution and major steps of calcareous cnidarian development in the Palaeozoic and Mesozoic. Thick black lines indicate the end-Permian (251 Ma) and the end-Cretaceous (65 Ma) extinction events. See text for details.

Scleractinia arrived late in Earth's history during the Middle Triassic Anisian stage about 237 Ma (Fig. 6.1; Stanley & Fautin, 2001). These earliest scleractinian corals were discovered in coeval sedimentary units in the Guizhou province of southern China (Deng & Kong, 1984; Qi, 1984) and from the Cracow-Silesia region in central Europe (Morycowa, 1988). These two widely separated places yielded a surprisingly diverse and well differentiated coral community of nine to ten families, which raises questions about their ancestry (Stanley, 1988; Roniewicz & Morycowa, 1993). A broad account of the earliest Anisian and Late Triassic coral occurrences is provided in Flügel (2002).

Other framework-forming cnidarians, including some major reef-builders, existed further back to the Palaeozoic before the rise of the scleractinians. The Rugosa appeared as simple solitary growth forms in the Ordovician and diversified later forming many colonial forms (see Fig. 6.1; Scrutton, 1997). Almost all rugose corals had calcitic skeletons. The second calcified group of Palaeozoic cnidarians, the Tabulata, was an exclusively colonial order that appeared 'suddenly' in the earliest Cambrian with members of many genera (Fig. 6.1; Lafuste *et al.*, 1991). Although not yet well defined, the mineralogy of tabulate corals is believed to be calcitic. Both orders, the Rugosa and the Tabulata, became extinct during the Earth's worst mass extinction at the end of the Permian about 251 million years ago (the Permian–Triassic extinction, see Fig. 6.1). The first Scleractinia arose suddenly 14 million years later. The Permian–Triassic extinction event wiped out over 90% of marine species and 70% of terrestrial vertebrate genera (Erwin, 1994) and happened at a time when almost all the Earth's continents were assembled to form the giant Pangaea supercontinent. Compared to other global mass extinction events in Earth's history, the Permian–Triassic crisis was followed by an unusually long aftermath, throughout the entire Early Triassic, until ecosystems recovered during the Middle Triassic. The geological record indicates that carbonate platform sedimentation, skeletal biota and reef systems were all suppressed in the Early Triassic (Flügel, 2002). The only exception in terms of carbonate precipitation in the Early Triassic is microbialite growth along the shores of the tropical Tethys Ocean (Kershaw *et al.*, 2007). This period is clearly characterised as a time of environmental perturbations that affected the global carbon–carbonate cycle with unusual seawater chemistry, and very probably also changes in the composition of the atmosphere (Knoll *et al.*, 1996; Fraiser & Bottjer, 2007).

The interpretation of the devastating Permian–Triassic crisis is complex and contentious. For example, Knoll *et al.* (1996) suggested that these marine mass extinctions could have been driven by overturning of deep, anoxic waters rich in both hydrogen sulfide and carbon dioxide. This would have had devastating effects on the physiology of marine organisms by poisoning and distorting the acid–base equilibrium of their body fluids under elevated CO_2 (hypercapnia). Elevated CO_2 in the seawater also lowers both pH and carbonate levels, see Topic box 7.1, p. 214. This may have induced a biocalcification crisis on top of the already severe long-term oceanic conditions (Fraiser & Bottjer, 2007). In the last stages of the Permian and through the Early Triassic, atmospheric CO_2 levels were elevated by perhaps 1000–1500 ppm (Berner, 2002), most likely triggered through the outgassing from giant continental flood basalt provinces such as volcanism from the Siberian Trap (Wignall, 2001). In comparison, the modern CO_2 concentration in the atmosphere climbed from about 280 ppm at the beginning of the industrial era to about 385 ppm today and is projected to reach 540–970 ppm by 2100 (Prentice *et al.*, 2001) leading Guinotte *et al.* (2006) to forecast the spread of carbonate-undersaturated deep waters and the decline of modern cold-water coral habitats (see discussion of 'ocean acidification' in Section 8.1.4, p. 247). The Permian–Triassic crisis decimated major carbonate-secreting orders, including the rugose and tabulate corals. The 14 million year gap in carbonate deposition during the Early Triassic strongly suggests that radical changes in the carbonate chemistry of seawater had devastating effects on calcifying organisms during this period of Earth's history. The Middle Triassic then ushered in a beneficial phase for aragonite-secreting organisms leading to the sudden emergence of the Scleractinia (Fig. 6.1). But were they in fact so sudden to appear?

Many palaeontologists try to relate the ancestry of the Scleractinia with Palaeozoic holdovers from some rugose corals with scleractinian affinities (Schindewolf, 1942; Cuif, 1981). The so-called scleractiniamorphs, like the Permian aragonitic coral *Numidiaphyllum gillianum*, have also been discussed as potential ancestors (Fig. 6.1; Wendt, 1990; Ezaki, 2000). This peculiar solitary coral has a scleractinian-like symmetry and a cyclic pattern of septal insertion (Ezaki, 1998). Older scleractiniamorphs occurred in the Middle Ordovician with the kilbuchophyllids (Scrutton, 1993) and the Mid-Permian *Houchangocyathus* (Ezaki, 2000), see Fig. 6.1.

Stanley and Fautin (2001) questioned the importance of skeleton formation as an essential taxonomic attribute and introduced the 'naked coral' hypothesis. Conventional classification schemes in scleractinian families evaluate gross skeletal features (e.g. Wells, 1956) and the ultrastructural elements of the coral skeleton (e.g. Roniewicz, 1996) to explain relationships between different orders, families or genera. These approaches widely accept a monophyletic origin of the Scleractinia, implying that all members derived from a single ancestor. This view was challenged when molecular genetic investigations inferred a polyphyletic evolution of the Scleractinia with at least two different lineages of scleractinian ancestors (the 'robust' and 'complex' clades), see Section 2.5, p. 55, Romano and Cairns (2000) and discussion in Stanley (2003). Molecular clock data, calibrated against the fossil record, suggest that two major ancestral groups diverged about 300 million years ago in the Late Carboniferous (see Fig. 6.1).

Among the non-calcifying Cnidaria, the Corallimorpharia (corallimorphs) and Actiniaria (sea anemones) share soft tissue characteristics with the Scleractinia (particularly the arrangement of mesenteries, see Section 3.1, p. 68) and are also closely related in terms of radioimmunoassay analyses (Buddemeier & Fautin, 1996). Based on mitochondrial genome sequencing, corallimorphs are more closely related to complex clade scleractinians than robust clade scleractinians, implying that the corallimorphs evolved from a calcified coral ancestor but subsequently lost their skeletons (Medina *et al*., 2006). However, non-calcified anemone-like lineages have left only trace fossils in the sedimentary record. Interestingly, several trace fossil types were assigned to anemone-like cnidarians in Palaeozoic sediments, and conspicuous trace fossils were also known from Early Triassic rocks (Stanley, 1988). The naked coral hypothesis goes beyond the soft-bodied ancestry in scleractinian corals as it regards skeleton formation as ephemeral. This view implies that calcification is a response to major shifts in seawater chemistry such as variations in Mg/Ca ratios, alkalinity and saturation states of calcium carbonate (Payne *et al*., 2004; Stanley, 2006).

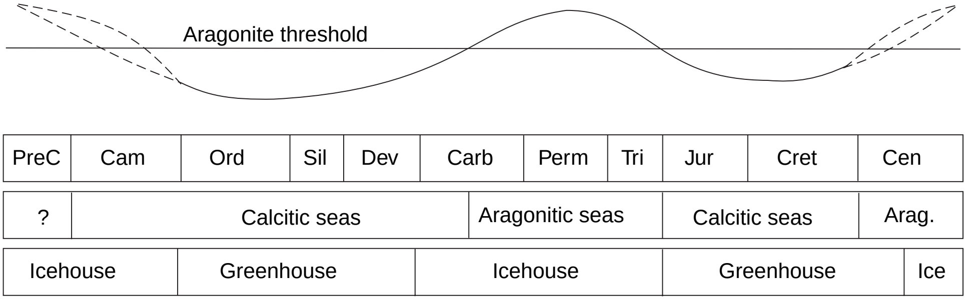


Fig. 6.2. Sandberg curve showing changes in the dominance of calcitic and argonitic biomineralisation strategies by marine organisms through time. Strategies adopted are controlled by global climate and related ocean acidity. Figure redrawn from Sandberg (1983) with permission of Nature Publishing Group.

Thought of in this way, calcification is a by-product rather than a prerequisite to define scleractinian corals as a phylogenetic entity. This hypothesis would also explain another stumbling block in palaeontology – the so-called Lazarus taxa phenomenon. Some Late Triassic taxa, including coralline and hexactinellid sponges and gastropods, correspond to Permian genera but were not documented in the Early to Middle Triassic (e.g. Flügel, 2002). Is this gap in the fossil record an artefact because they have yet to be discovered? Might contemporaneous sedimentary sequences have been lost through subduction? Or could it be that the variations in seawater carbonate chemistry described above led to periods when 'corals' existed with and without skeletons?

The Sandberg curve and models derived from it (Fig. 6.2) provide the environmental background for such provocative thoughts on the ephemeral nature of the skeleton in scleractinian corals (Sandberg, 1983; Stanley & Hardie, 1998; Stanley, 2006). Plate tectonics determine the levels of global volcanism and uplift-induced weathering, which further controls global CO_2 input and absorption respectively. The plate tectonically-induced oscillations in pCO_2 brought about long-lasting changes in global conditions between greenhouse and icehouse climates. In line with that, pCO_2 also affects ocean 'acidity' and the ability of organisms to biomineralise calcite and aragonite (aragonite being more soluble and so more vulnerable to increased ocean acidity). Medina *et al.* (2006) proposed that the corallimorphs originated in the Late- to Mid-Cretaceous (110–132 Ma) at a time coinciding with high levels of oceanic CO_2 and calcitic seas (Fig. 6.1) when many scleractinians became extinct (Buddemeier & Fautin, 1996). The Sandberg curve eloquently explains the dominance of calcite- or aragonite-rich biomineralogies in the marine realm during the Phanerozoic. An aside to this is the concern that we may now, due to anthropogenically induced increases in pCO_2, be at another flexure in the Sandberg curve risking a change back to calcitic seas with all the implications that has for aragonitic cold-water corals (see discussion of ‘ocean acidification’ in Section 8.1.4, p. 247).

As mentioned above, the earliest scleractinian corals appeared during the Anisian stage of the Middle Triassic, 14 Ma after the devastating events of the Permian–Triassic extinction. These corals already showed remarkable diversity and colonial integrity. Their appearance, in what is today southern China, coincides with the first post-crisis development of carbonate shelves indicating that marine ecosystems were recovering. While scleractinian corals thrived in tropical latitudes they were of little importance in reef framework construction and more common in deeper, offshore waters (Flügel, 2002).

The predominant, though not unchallenged, view is that Anisian corals were azooxanthellate, based on indirect characteristics like the degree of their colonial integrity and phaceloid growth with large corallites (Stanley, 1981). The first coral-rich reefs boomed 15–20 Ma later in the Norian-Rhaetian stages of the Late Triassic at a time that coincides with the advent of scleractinian–zooxanthellae symbiosis (Fig. 6.1; Wood, 1993; Fensome *et al.*, 1998). Indeed, Stanley and Swart (1995) were able to discern zooxanthellate isotopic signatures from pristinely preserved aragonitic scleractinians of Late Triassic age. Stable isotope samples from azooxanthellate coral skeletons always show a strong positive correlation between $\delta^{13}C$ and $\delta^{18}O$ isotopes, whereas no such strong correlation exists in zooxanthellate corals (Swart, 1983; and see Section 7.1.2, p. 218). Isotope signatures characteristic of azooxanthellate corals were found in two Late Jurassic species from Poland (*Thamnasteria concinna* and *Actinaraeopsis exilis*), both interpreted as being from cold-water settings (Roniewicz, 1984; Gruszczynski *et al.*, 1990). However, such straightforward geochemical methods depend on the preservation of pristine aragonitic skeletons without diagenetic alteration of stable isotope ratios. Calcite is the more stable crystal form of calcium carbonate and in a vadose environment (the zone between the groundwater table and the land surface) aragonite eventually recrystallises to calcite (James, 1974). Fossil aragonitic corals have often been found as re-worked skeletons transported from the photic zone (in case of zooxanthellate corals) to deeper water settings where burial in pelagic or hemipelagic muds halted or delayed this diagenetic conversion in the marine environment.

6.2 Fossil record of cold-water corals

The evolutionary history of the Scleractinia during the Mesozoic saw a series of radiation and extinction events. In turn, the contribution of reef systems to geological sequences changes and different framework-building species are associated with each event. We recommend the review by Stanley (2003) and the seminal special volume, edited by Kiessling *et al.* (2002), for details on shallow-water reef evolution and the Scleractinia. We focus here on the azooxanthellate cold-water coral frameworks in the post-Triassic, Mesozoic and Cenozoic.

The Jurassic period (199 to 145 Ma; see Fig. 6.1) saw aphotic bioherms formed by microbial mud mounds in the Early Jurassic, by siliceous sponge mounds in the Middle Jurassic and by pure microbialite mounds in the Upper Jurassic (Leinfelder *et al.*, 2002). This does not imply that corals did not occur in deeper waters but if they did they probably lacked framework-building capacities. However, by the Cretaceous we start to see the first deep-water thickets and mounds of azooxanthellate corals. These were primarily constructed from a few genera of the Dendrophylliidae and Oculinidae. The Caryophylliidae, which evolved to become the most diverse family of azooxanthellate and deep-water genera, built the most recent deep-water frameworks in the Cenozoic period. At the Cretaceous–Tertiary boundary (65 Ma, Figs. 6.1 and 6.3), dramatic events created a mass extinction among the marine and terrestrial biota including 45% of Late Cretaceous scleractinian coral species (Kiessling & Baron-Szabo, 2004). Also known as the K–T boundary, this most famous of all mass extinctions, which also saw the demise of the dinosaurs, has been related to a large meteorite impact near the town of Chicxulub in the present-day Yucatan peninsula of Mexico (Kring, 2007). According to Kiessling and Baron-Szabo's careful statistical approach, zooxanthellate corals suffered more extinctions than azooxanthellate species with colonial forms affected more than solitary. Azooxanthellate corals in higher latitudes were more resistant to extinction, with this group evolving into many more new genera in the Danian (65–61 Ma, Fig. 6.3) than the zooxanthellates. However, about four million years later in the Late Palaeocene period, the zooxanthellate corals had attained equivalent diversity (Kiessling & Baron-Szabo, 2004).

6.2.1 Dendrophylliidae

This family comprises 166 living species (149 azooxanthellate) grouped in 31 fossil and extant genera with 16 being colonial forms (Cairns, 2001b; Filkorn & Pantoja Alor, 2004; see Online Appendix at www.lophelia.org/coldwatercorals-book). The most distinctive feature of the dendrophylliids is their porous thecal wall, called a synapticulotheca (Cairns, 2001b). Dendrophylliids are known from the Early Cretaceous Barremian stage, about 122 Ma (Fig. 6.3), with the solitary *Palaeopsammia* as the oldest representative genus of this group. The first colonial dendrophylliid was *Blastozopsammia* from approximately 100 million-year old deposits of the Early Cretaceous Albian stage (Fig. 6.3; Filkorn & Pantoja Alor, 2004). Shortly after the Cretaceous–Tertiary boundary, the genus *Dendrophyllia* evolved in the Danian, 65–61 Ma in the boreal high northern latitudes of Greenland, Denmark and Sweden (Floris, 1972), see Fig. 6.3. This region formed

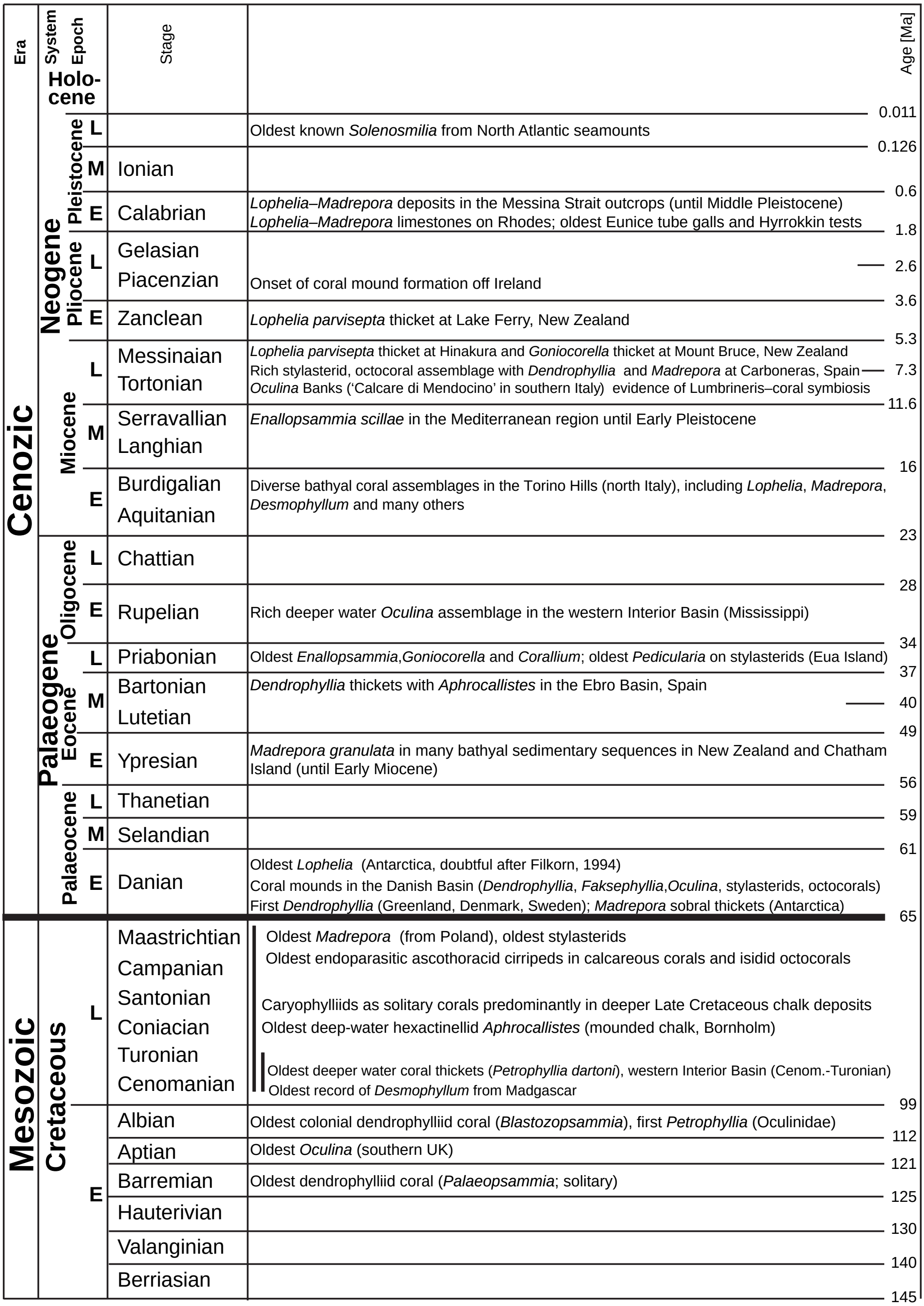


Fig. 6.3. Temporal evolution of cold-water corals (Dendrophylliidae, Oculinidae, Caryophylliidae, emergence of Stylasteridae, Isididae and *Corallium*) and major fossil sites from the Mesozoic to the present. Age indications derived from Gradstein *et al.* (2004). The bold line at 65 Ma marks the position of the end-Cretaceous mass extinction event. See text for details. E, Early; M, Middle; L, Late.

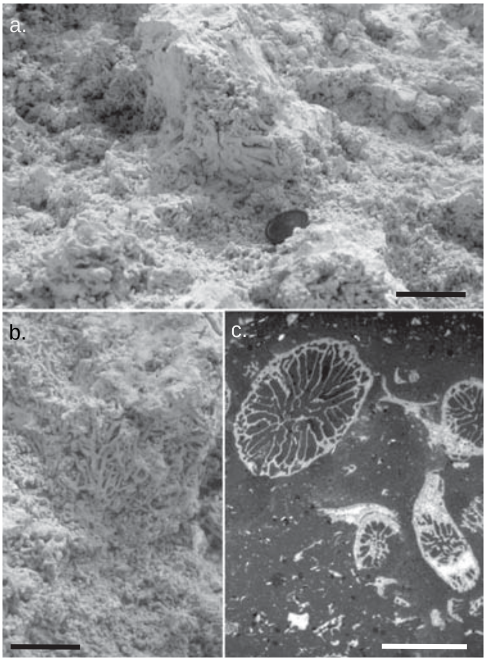


Fig. 6.4. Photographs (a) and (b) show the coral limestones from the Fakse outcrop in Denmark. These represent true coral mounds constructed by the dendrophylliids *Dendrophyllia candelabrum*, *Faksephyllia faxoensis* and by the oculinid *Oculina becki*. (c) Petrographic thin section with *Dendrophyllia* (upper left) and *Oculina* (right) embedded in a fine-grained carbonate mud matrix. Scale bars 20 cm in (a) and (b), 1 cm in (c). Images courtesy of M. Bernecker.

an epeiric seaway covering the Danish Basin, known for its aphotic, cool-water bryozoan (Bjerager & Surlyk, 2007a, 2007b) and coral mounds (Bernecker & Weidlich, 1990, 2005) in a continental shelf setting. Larger offshore coral mounds developed mostly on a topographic feature, the Ringkøbing-Fyn High, whereas smaller mounds developed closer to shore in shallower waters (Surlyk, 1997). Individual lenticular coral mounds attained lengths of 50–200 m, widths of 80 m and heights of 15 m to at least 30 m. The most abundant framework-forming coral was *Dendrophyllia candelabrum* with dendroid colonies up to 50 cm high (Bernecker & Weidlich, 1990), see Fig. 6.4. A thorough overview of fossil and extant dendrophylliid species is provided by Cairns (2001b).

The other extant dendrophylliid capable of framework construction in present deep-water environments is *Enallopsammia* (Table 6.1). This genus appeared shortly after *Dendrophyllia* and is known from the Late Eocene tuff deposits of Eua Island, Tonga with *Enallopsammia laddi* as the oldest representative (Fig. 6.3; Wells, 1977). A Middle Miocene *Enallopsammia* species, *E. poppelacki*, was found in northern Italy and continued into the Late Miocene (Tortonian) of northern Italy,

Table 6.1 *Fossil record of dendrophylliid (*Enallopsammia*) and oculinid (*Oculina, Madrepora*) corals (E = Early, M = Middle, L = Late, * = larger thicket preservation). The absolute ages for the stratigraphic epochs and stages are given in Figs. 6.1 and 6.3.*

Species	Stage/Epoch	Location	Main reference
***Enallopsammia** laddi*	Priabonian/ L. Eocene	Eua Island, Tonga	Wells (1977)
E. sp.	E. Miocene	Mount Cerberus, NZ	Wells (1977)
E. scillae	M. Miocene to E. Pleistocene	Torino Hill & Sicily, Italy	Seguenza (1864); Chevalier (1961)
E. poppelacki	Tortonian/ L. Miocene	Torino Hill, Italy & Vienna Basin, Austria	Chevalier (1961)
***Oculina** hobleyi*	Aptian/E. Cretaceous	South England, UK	Casey (1961)
O. nefrens	Albian/E. Cretaceous	Koranga River, NZ	Speden (1975)
O. sp.	Santonian/ L. Cretaceous	Conway River, NZ	Warren & Speden (1978)
O. nordenskjoeldi	L. Campanian to Maastrichtian	Seymour Island, Antarctica	Filkorn (1994)
*O. becki**	Danian-Selandian/ Palaeocene	Nugssuaq, Greenland	Floris (1972)
O. smithi	Palaeocene	Wilcox County, Alabama, USA	Toulmin (1977)
O. alabamensis	Selandian-Thanet./ Palaeocene	Greggs Landing, Alabama, USA	Toulmin (1977)
O. oamurensis	E. Eocene to M. Oligocene	New Zealand	Squires (1958)
O. singleyi	Lutetian/M. Eocene	Texas, USA (several sites)	Vaughan (1900)
O. conferta	Priabonian/L. Eocene	Cliffend, Hampshire, UK	Burton (1933)
O. vicksburgensis	Rupelian/ E. Oligocene	Vicksburg, Mississippi, USA	Vaughan (1900)
O. mississippiensis	Rupelian/ E. Oligocene	Vicksburg, Mississippi, USA	Vaughan (1900)
O. harrisi	Rupelian/ E. Oligocene	Vicksburg, Mississippi, USA	Vaughan (1900)
O. aldrichi	Rupelian/ E. Oligocene	Byrams Ferry, Mississippi, USA	Vaughan (1900)
O. panzana	L. Oligocene to E. Miocene	California, USA	Loel & Corey (1932)
O. virgosa	E. Miocene-Recent	many sites in New Zealand	Squires (1958); Cairns (1995)

Table 6.1 (*cont.*)

Species	Stage/Epoch	Location	Main reference
O. sp.	Tortonian/ L. Miocene	Calabria, Italy	Mastandrea *et al.* (2002)
Madrepora sp.	Maastrichtian/ L. Cretaceous	Blizow, Poland	Stolarski & Vertino (2007)
*M. sobral**	Danian/ E. Palaeocene	Seymour Island, Antarctica	Filkorn (1994)
[*M. granulata*]	[E. Eocene to L. Miocene]	[New Zealand, Chatham Is.]	Squires (1958); Kear & Schofield (1978); Campbell *et al.* (1993)
M. sp.*	Eocene	Mah Tug & Bosti, Somalia	Latham (1929)
M. natchitochensis	Lutetian/ M. Eocene	Natchitoches, Louisiana, USA	Vaughan (1900)
M. sp.*	Priabonian/ L. Eocene	Eua Island, Tonga	Wells (1977)
M. solanderi	Priabonian/ L. Eocene	Cliffend, Hampshire, UK	Burton (1933)
M. sp.	E. Miocene	Magar Pir, Pakistan	Duncan (1880)
M. profunda	Burdigalian/ E. Miocene	Torino Hill, Piedmont, Italy	Chevalier (1961)
M. reflexa	Burdigalian/ E. Miocene	Torino Hill, Piedmont, Italy	Chevalier (1961)
M. compressa	Burdigalian/ E. Miocene	Torino Hill, Piedmont, Italy	Chevalier (1961)
M. michelotti	Burdigalian/ E. Miocene	Torino Hill, Piedmont, Italy	Chevalier (1961)
M. moravica	Burdigalian/ E. Miocene	Torino Hill, Piedmont, Italy	Chevalier (1961)
M. quenstedti	Burdigalian/ E. Miocene	Torino Hill, Piedmont, Italy	Chevalier (1961)
M. palmata	Burdigalian/ E. Miocene	Charles County, Maryland, USA	Bouchet *et al.* (2005)
M. duncani	M. Miocene to L. Miocene	Java	Gerth (1933); Osberger (1954)
M. sp.	Messinian/ L. Miocene	Carboneras, Spain	Barrier *et al.* (1991)
M. squarrosa	Pliocene	Geger Tjabe, Java	Osberger (1954)

the Czech Republic and the Vienna Basin (Cairns, 2001b). *Enallopsammia scillae* appeared during the Middle Miocene of Italy (Chevalier, 1961) and, more abundantly, in the Plio-Pleistocene bathyal marls of Sicily (Seguenza, 1864; Di Geronimo *et al*., 2005). *Enallopsammia rostrata* and *E. profunda* are considered Holocene species (Cairns, 2001b), see Section 2.2.1, p. 30.

6.2.2 Oculinidae

This family consists of ten exclusively colonial genera and first appeared in the Early Cretaceous Aptian stage, about 125–112 Ma (see Fig. 6.3) as *Oculina hobleyi* (Casey, 1961) (Table 6.1). The genus *Oculina* is apozooxanthellate as some species have the capacity for zooxanthellate symbiosis in the photic zone but can live without symbionts under aphotic conditions (Stanley & Cairns, 1988). The modern *Oculina varicosa* is just such a facultatively zooxanthellate coral forming both shallow-water zooxanthellate colonies and azooxanthellate deep-water coral reefs off Florida (Reed, 2002). It is one of the few cold-water corals from which information on reproduction and larval biology has been gathered (see Section 3.7, p. 105).

Oculina has a rich fossil record during the Cenozoic period (Table 6.1). Shortly after the Cretaceous–Tertiary Boundary extinction event, *Oculina becki* appeared in the Danian deeper water environments of Nugssuaq, west Greenland (Floris, 1972) and in southern Scandinavia, where this species contributed to coral mound formation (see Fig. 6.4; Bernecker & Weidlich, 2005). Cold-water palaeostrait deposits in northern Calabria have revealed large cold-water coral banks of Tortonian age (12–7 Ma) with *Oculina* as the major framework-forming coral (Mastandrea *et al*., 2002).

The genus *Petrophyllia*, the senior synonym of *Archohelia*, appeared in the Albian 112–99 Ma (see Fig. 6.3) and survives with the sole known extant and azooxanthellate representative, *Petrophyllia rediviva*, off the Queensland coast of eastern Australia (Wells & Alderslade, 1979). *Petrophyllia dartoni* lived in the western Interior Basin of North America from the Cenomanian to Turonian stage of the Mid-Cretaceous, about 99–89 Ma (H. F. Filkorn, personal communication, 2008). This species is exceptional, as it formed the only known deep-water coral thickets in the Cretaceous (Coates & Kauffman, 1973). The small thicket is exposed near Lamy, New Mexico, USA and measures just 18 cm in thickness.

The third genus with a framework-forming capacity, currently placed within the Oculinidae, is *Madrepora*. However, phylogenetic studies by Le Goff-Vitry *et al*. (2004b), suggested a new grouping lying between the Caryophylliidae and the Pocilloporidae, probably at familial or even higher systematic level (see Section 2.5, p. 55). Stolarski and Vertino (2007) extended the date for the first appearance of *Madrepora* back into the Early Maastrichtian (Late Cretaceous, 70 Ma) of Poland (Fig. 6.3 and Table 6.1). The corals are preserved as imprints in siliceous deep-water limestones. Only dispersed specimens were found, indicating that small colonies were present rather than larger thickets (Stolarski & Vertino, 2007). The next stratigraphic occurrence of *Madrepora* is from the Early Palaeocene Sobral Formation of Seymour Island, Antarctica (Filkorn, 1994). The preservation and depositional style of *Madrepora sobral* indicate the presence of larger coppices or thickets. Table 6.1 lists further Cenozoic fossil *Madrepora* of which the two Eocene sites in Somalia and on Eua Island, Tonga represent former coral thickets.

6.2.3 Caryophylliidae

As discussed in Section 2.2.1, p. 26, the most diverse azooxanthellate scleractinian clade is the Caryophylliidae with 294 living species (see Table 2.2 and Online Appendix at www.lophelia.org/coldwatercoralsbook). Extant deep-water reef framework-forming corals from this group are *Lophelia, Solenosmilia* and *Goniocorella*. Caryophylliids first appeared in inner shelf settings about 183–176 Ma during the Toarcian stage of the Early Jurassic (see Fig. 6.1). Within the first five million years of their history, they expanded to the outer shelf but only at low diversities. Their diversity increased during the Late Jurassic period and species spread over the continental shelves during the Cretaceous and were especially common in Late Cretaceous chalk deposits, mainly as solitary corals. Their spread into the bathyal zone became evident from the Early Cenozoic (Fig. 6.3; Droser *et al.*, 1993).

The first occurrence of the genus *Lophelia* is not well constrained in the rock record. Two Early Palaeocene occurrences of *Lophelia*, one from west Greenland and the other from Seymour Island, Antarctica, are often cited in the literature, but the authors, Floris (1972) and Filkorn (1994), treat their *Lophelia* findings with some caution as these are based on a few, badly preserved fragments (Table 6.2 and Fig. 6.3). Squires (1957) described and illustrated *Lophelia tubaeformis* from an outcrop coppice near Bainbridge, Georgia, USA. However, the geological age of this outcrop is uncertain as it contains a mélange of Eocene and Oligocene fossils. To date, the most reliable *Lophelia* occurrence derives from a Late Miocene coral thicket at Hinakura, New Zealand (Squires, 1964), see Colour plate 25. The thicket was constructed solely from a single *Lophelia* species, described as *Lophelia parvisepta* (Tenison-Woods, 1880). Squires (1964) noted that *Lophelia parvisepta* formed massive, thick-walled, intricately branched skeletons with short calices. The thicket grew upon a flat, hardened mudstone seabed and reached a thickness of 3.4 m in the central part of the 36.6 m long exposure. A second *L. parvisepta* thicket is known as the Lake Ferry

Table 6.2 *Fossil record of caryophylliid (*Lophelia, Goniocorella, Desmophyllum*) corals (E = Early, M = Middle, L = Late, * = larger thicket preservation). The absolute ages for the stratigraphic epochs and stages are given in Figs. 6.1 and 6.3.*

Species	Epoch/Substage	Site	Reference
Lophelia sp. (?)	Danian/E. Palaeocene	Nugssuaq, Greenland	Floris (1972)
L. sp. (?)	Danian/E. Palaeocene	Seymour Island, Antarctica	Filkorn (1994)
L. tubaeformis	Eocene or Oligocene	Flint River, Georgia, USA	Squires (1957)
L. sp. (?)	E. Miocene	Djunggrangan area, Java	Osberger (1954)
[*L. defrancei*]	[M. Miocene to E. Pliocene]	[Sardinia & Sicily]	De Angelis d'Ossat & Neviani (1897)
*L. parvisepta**	L. Miocene to E. Pliocene	Palliser Bay, NZ	Squires (1964)
Goniocorella *eguchii*	Priabonian/L. Eocene	Eua Island, Tonga	Wells (1977)
*G. dumosa**	L. Miocene-Recent	Mount Bruce, NZ	Wells (1986)
Desmophyllum *cylindricum*	Cenomanian/ L. Cretaceous	Madagascar	Collignon (1931)
D. sp.	E. Maastrichtian/ L. Cretaceous	Overstrand, Norfolk, UK	Mortimore *et al.* (2001)
D. sp.	Danian/E. Palaeocene	Nugssuaq, Greenland	Floris (1972)
D. sp.	Lutetian/M. Eocene	Hampden, NZ	Squires (1958)
D. castellolense	Bartonian/L. Eocene	Igualada, Spain	Alvarez-Perez (1997)
D. deculpum	Priabonian/L. Eocene	Eua Island, Tonga	Wells (1977)
D. lirioides	Priabonian/L. Eocene	Eua Island, Tonga	Wells (1977)
D. coulsoni	Priabonian/L. Eocene	Eua Island, Tonga	Wells (1977)
D. bilobatum	Burdigalian/ E. Miocene	Torino Hill, Piedmont, Italy	Chevalier (1961)
D. cantamessai	Burdigalian/ E. Miocene	Torino Hill, Piedmont, Italy	Chevalier (1961)
D. conulatum	Burdigalian/ E. Miocene	Torino Hill, Piedmont, Italy	Chevalier (1961)
D. exclavatum	Burdigalian/ E. Miocene	Torino Hill, Piedmont, Italy	Chevalier (1961)
D. formae	Burdigalian/ E. Miocene	Torino Hill, Piedmont, Italy	Chevalier (1961)

Table 6.2 (*cont.*)

Species	Epoch/Substage	Site	Reference
D. nudum	Burdigalian/ E. Miocene	Torino Hill, Piedmont, Italy	Chevalier (1961)
D. reussanum	Burdigalian/ E. Miocene	Torino Hill, Piedmont, Italy	Chevalier (1961)
D. semicostatum	Burdigalian/ E. Miocene	Torino Hill, Piedmont, Italy	Chevalier (1961)
D. striatum	Burdigalian/ E. Miocene	Torino Hill, Piedmont, Italy	Chevalier (1961)
D. taurinense	Burdigalian/ E. Miocene	Torino Hill, Piedmont, Italy	Chevalier (1961)
D. turgidum	Burdigalian/ E. Miocene	Torino Hill, Piedmont, Italy	Chevalier (1961)
D. ambiguum	Tortonian/ L. Miocene	Tortona, Piedmont, Italy	Chevalier (1961)
D. dertonensis	Tortonian/ L. Miocene	Tortona, Piedmont, Italy	Chevalier (1961)
D. productum	Tortonian/ L. Miocene	Tortona, Piedmont, Italy	Chevalier (1961)
D. sp.	Messinian/ L. Miocene	Carboneras, Spain	Barrier *et al.* (1991)

Thicket, formerly exposed in a sea cliff on the northeast side of Palliser Bay (Squires, 1964), see Colour plate 25, and is of Early Pliocene age. In contrast to the Hinakura exposure, the *Lophelia* corallites here are thinly calcified and its branches are surmounted by tall trumpet-shaped calices. The thickets developed during sedimentation breaks on the surfaces of hardened mudstone sequences, which allowed coral settlement and initial rapid growth. Before reaching a better developed coppice stage, the young coral thickets were buried by re-activated deposition of mud and became preserved in place. Further *Lophelia* records remain rare (see Table 6.2) until the Plio-Pleistocene, when *Lophelia pertusa* became common in the Mediterranean and Atlantic. As discussed in Case study 4.1, p. 122, the coral carbonate mounds off Ireland in the northeast Atlantic started to develop more or less contemporaneously in the Late Pliocene, about 2.7 Ma years ago, at a period when northern hemisphere glaciations commenced along with the formation of the modern water mass stratification in the northeast Atlantic. Thus, *Lophelia* was at least present in the Late Miocene of the southwest Pacific (New Zealand) and since the Late Pliocene in the northeast Atlantic and even later during the Early Pleistocene in the Mediterranean Sea. All Miocene Mediterranean, and older *Lophelia* records elsewhere, should be treated with caution.

Case Study 6.1 **The Mediterranean cliff-bound coral habitat**

Compared to the passive continental margins of the North Atlantic, wide and gently inclined shelves are rarely developed in the Mediterranean Sea (Vanney & Gennesseaux, 1985). Instead, steep, fault-bounded submarine escarpments and canyons have been characteristic features in bathyal Mediterranean coral habitats since the Miocene (Barrier *et al.*, 1991; Mastandrea *et al.*, 2002; Titschack *et al.*, 2005), Fig. 6.5. In the geodynamically active Mediterranean even bathyal sedimentary sequences were rapidly uplifted to form land over less than 2 million years. Various outcrops in southern Italy, Sicily and Rhodes probably yield the largest and best exposed bathyal cold-water coral outcrops in the world (Fig. 6.6 and Colour plate 26). Major outcrop areas are found on both sides of the Messina Strait, separating the peninsula of southern Italy from Sicily. The geodynamic evolution of the Calabro-Peloritan Arc created rapid subsidence of fault blocks from littoral to bathyal depths of about 600–1000 m depth beginning 4 million years ago in the Early Pliocene and climaxing about 0.9 Ma in the Early Pleistocene (Montenat *et al.*, 1991).

Fig. 6.5. Artist's reconstruction of a cliff-bound cold-water coral setting characteristic of many Cenozoic and Recent *Lophelia–Madrepora* occurrences from canyon walls and steep escarpments in the Mediterranean Basin. Note the coral debris falls accumulating on the seafloor beneath the live colonies. Illustration derived from an original figure by J. Titschack.

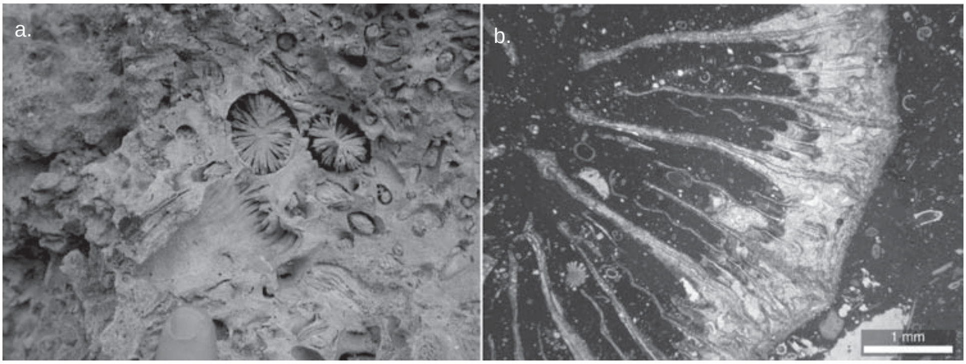


Fig. 6.6. Different preservation of Early Pleistocene *Desmophyllum dianthus*. (a) La Montagna near Messina, Sicily: complete aragonite dissolution has left behind a mouldic preservation with the external imprint of a corallite (below) and the calcitic mud sediment infill into two corallites (above). (b) Capo dell Armi near Reggio Calabria, southern Italy: thin section showing pristine corallite preservation of a *Desmophyllum* corallite with all details of the septal insertion, embedded within a hemipelagic calcareous mud. Images courtesy of J. Titschack.

Case Study 6.1 (cont.)

During the advent of the remaining Pleistocene, compressional tectonic plate movements caused rapid uplift of the strait margins. Today, bathyal sediments are exposed at elevations of 400 m above sea level along the Messina Strait margins. The fault-bounded, steep escarpments of the strait provided the habitat for bathyal coral communities. The coral communities can be found on their original substrata such as cliffs, escarpments and detached boulders, locally fringed by thick coral debris wedges (e.g. Barrier *et al*., 1996). For more information, we recommend the review of temporal evolution of cold-water corals by Taviani *et al*. (2005).

The geological history of *Solenosmilia variabilis* is not known. The only available information is from Schröder-Ritzrau *et al*. (2005) who provided some Late Pleistocene U/Th ages for this species collected from several seamounts in the central northeast Atlantic (see Fig. 6.3).

The fossil record of *Goniocorella* is also rather poor (Table 6.2). Several specimens of *Goniocorella eguchii* are described from Late Eocene tuff deposits on Eua, Tonga (Wells, 1977). The second documentation of this genus is from the Late Miocene Mangaoranga Formation at Mount Bruce, New Zealand (Wells, 1986). The Miocene *Goniocorella* is a thicket occurrence and resembles the extant *Goniocorella dumosa* in all morphological characteristics.

Among the many solitary caryophylliid azooxanthellate corals, *Desmophyllum dianthus* (Fig. 6.6 and Colour plate 26) deserves recognition here as it very often occurs with *Lophelia, Madrepora* and *Enallopsammia* as an associated species. In some places, *Desmophyllum* forms dense aggregations, preferably underneath rock ledges on steep escarpments or other forms of erosional scars on the seabed (e.g. Försterra *et al*., 2005). With an annual skeletal growth rate of 0.5–2 mm yr^{-1}, *Desmophyllum* is a slow-growing coral with a lifespan of about 100 years (Adkins *et al*., 2004) see Table 3.2, p. 84. These characteristics make this species a prime candidate for palaeoenvironmental studies in the deep sea (see Fig. 7.4, p. 217 and discussion in Chapter 7). The fossil record extends back to the Late Cretaceous with findings from Madagascar (Cenomanian, 99–93 Ma) and Norfolk, UK (Early Maastrichtian, 71–70 Ma) (Collignon, 1931; Mortimore *et al*., 2001; Table 6.2 and Fig. 6.3). Early Cenozoic *Desmophyllum* were collected in Danian (65–61 Ma) deposits of west Greenland, Middle Eocene (49–40 Ma) deposits from New Zealand, and from the Middle to Late Eocene in Spain and Tonga (40–34 Ma) (see Table 6.2 for details). Except for the Spanish locality, all other *Desmophyllum* fossils were associated with bathyal coral communities.

To summarise, current knowledge tells us that the majority of the modern cold-water coral reef framework-formers appeared during the Cretaceous (e.g. *Oculina, Petrophyllia, Madrepora*) and by the Early Cenozoic at the latest (e.g. *Lophelia, Dendrophyllia, Enallopsammia, Goniocorella*). A similar trend is observed in the fossil record of the skeletonised deeper water hydrozoans and octocorals, which appeared in the Late Cretaceous (Voigt, 1958; Zibrowius & Cairns, 1992), see Fig. 6.3.

The palaeoecology of ancient cold-water coral assemblages is a short story in palaeontological terms spanning a mere 65 million years of the Cenozoic. Even so, the fossil record of cold-water coral frameworks remains patchy both stratigraphically and geographically. A significant increase of ancient cold-water coral systems occurred in the Late Pliocene to Early Pleistocene with a presumably concurrent formation of the hundreds, if not thousands, of coral carbonate mounds now known off Ireland and the rich coral occurrences in Calabria, Sicily and the Cook Strait, Lake Ferry, New Zealand. It is tempting to assume that within the geologically brief time span of just 2 to 3 million years, the previously 'dormant', though long-existing, cold-water coral genera suddenly mobilised to successively spread out along the continental margins. This period in Earth's history is marked by the onset of glaciations that include cyclic changes in both atmospheric climate and oceanographic currents, which evidently paved the way for cold-water corals to expand in deep, cold waters.

6.3 Taphonomy

Taphonomy analyses the entire history of organisms' remains following death, organic decay, sedimentation, burial and diagenetic alteration within the sediment column. The taphonomy of cold-water corals will differ from tropical corals because of key environmental differences, such as the absence of light at greater depths, lower ambient seawater temperatures, lower carbonate supersaturation and lack of tempestites (storm deposits). These factors create sedimentary facies in both ancient and modern cold-water reefs that are clearly different from their tropical counterparts. This second half of the chapter reflects on characteristic patterns and features that may help to identify yet undiscovered cold-water coral build-ups in the fossil record. As Stanley and Cairns (1988) pointed out, examples of fossil cold-water coral assemblages may go unrecognised by many field geologists due to the type of circular reasoning frequently inspired by rich deposits of corals – that the presence of coral remains indicates a warm-water, shallow environmental setting. We briefly recall basic criteria for recognition of cold-water coral build-ups in the fossil record based on the seminal papers by Teichert (1958), Squires (1964), Wilson (1979) and Mullins *et al.* (1981): (1) admixture of pelagic detritus (see Section 4.2, p. 112); (2) lack of an extensive contiguous shallow-water facies; (3) lack of coralline algae including photosynthetic bioeroders (see Section 6.3.2, below); (4) low diversity of primary reef framework-forming corals; (5) lenticular or mound-shaped geometries, often upon unconformities (see Section 4.5, p. 135); (6) unusual occurrences at high palaeo-latitudes; and (7) a stable oxygen and carbon isotope signature characteristic of azooxanthellate corals (see Section 7.1.2, p. 218).

6.3.1 Growth of the coral framework

Cold-water coral frameworks are characterised by an apparent low diversity of contributing corals. Only 17 species of the 711 azooxanthellate scleractinian corals can be regarded as framework forming (see Section 2.2.1, p. 25). Within any modern or fossil cold-water coral reef, only one or sometimes two or three species act as primary framework-formers. As the colony grows, the corals secrete branches bearing the individual corallites to generate a phaceloid or dendroid colony. Branches of neighbouring colonies that intermingle with the live corals may fuse together, supported by the calcification capabilities of the soft tissue coenenchyme, thus considerably enhancing the architectural stability and rigidity of the framework. Macroscopically, this coenenchyme expansion determines the thickness of the white, living zone of the coral coppices and may be a useful indicator of overall reef 'health'.

Epifaunal colonisation or fouling by other sessile organisms is apparently rare in the coenenchyme-covered parts of the colony, while on coenenchyme-barren coral skeleton, random larval spatfall of invertebrates increases diversity and secondary framework growth (see Case study 5.1, p. 147). The presence, expansion or withdrawal of the coenenchyme seems to vary over time but any patterns and underlying causes remain speculative. This behaviour may be related to physical disturbances, such as the removal or utilisation of settled particles within the live polyp zone (e.g. Wild *et al*., 2004). Biological factors influencing the extent of the coenenchyme could include pathogens causing viral, bacterial or fungal diseases, predatory grazing pressure (e.g. by asteroids) or allelochemical interactions of some specific organisms with the live corals (e.g. sponges) (Porter & Targett, 1988). Regardless of the causes of variable tissue expansion or retraction on the colony branches, it is the coenenchyme-triggered calcification that produces the formation of a micro-laminated thickening-deposit around the thecal wall (*sensu* Stolarski, 2003, formerly described as 'stereome' e.g. Sorauf, 1972). Wall thickening in species like *Lophelia pertusa* is a notably periodic phenomenon that produces distinct banding of dense and less dense layers viewed in cross-sections of the skeleton (Kaszemeik & Freiwald, 2002), see Fig. 6.7. The latter has a major affect on morphological plasticity in some azooxanthellate corals (Zibrowius, 1984). It seems that coenenchyme can regenerate over formerly tissue-barren coral framework, seal attached fauna beneath layers of thickened deposits (Harmelin, 1990; Beuck *et al*., 2007), see Fig. 6.7, and perhaps even inhibit competition from these colonists. The polychaete *Eunice* actively takes advantage of this peculiar calcification process in *Lophelia* and some other reef framework-forming cold-water corals by stimulating them to encalcify its parchment tube (see Section 5.4.1, p. 162). The coral–*Eunice* symbiosis can be traced back in the fossil record to at least the Early Pleistocene of the Mediterranean Sea (Titschack & Freiwald, 2005). The enormous calcification and antifouling capacities of the coenenchyme seem a vital factor in explaining the corals' competitive advantage over other hard substrata organisms.

6.3.2 Breakdown of the coral framework

In cold-water coral reefs, the breakdown of the framework is triggered by physical and biological processes that show both similarities and differences to those seen in shallow-water tropical reefs (Scoffin, 1981). Tropical reefs periodically experience severe storm events, causing substantial physical damage. Cold-water reefs thrive at depths beyond the storm-wave base (Frederiksen *et al*., 1992; Freiwald, 2002) but the hydrodynamic regime at the sites of cold-water coral reefs is anything other than quiet and sluggish (see Section 3.3.2, p. 77). However, large-scale

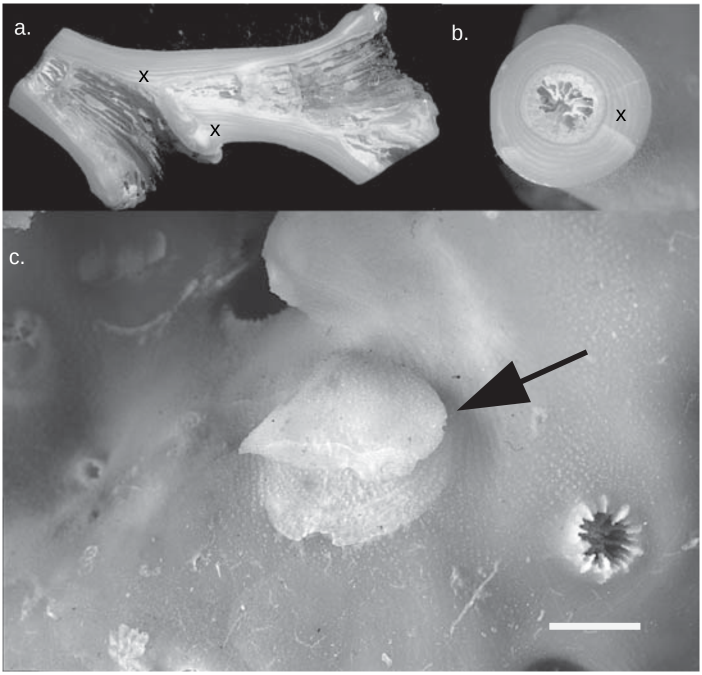


Fig. 6.7. The thickening deposits (×) that are periodically secreted by the coral's coenenchyme onto the corallite produce a characteristic banding pattern. (a) Longitudinal and (b) cross-sections of a polished *Lophelia pertusa* skeleton. (c) A cementing *Anomia* bivalve (arrowed) sealed by a faint aragonite layer from the *Madrepora* coenenchyme after settling on the coral skeleton. This *in situ* fixation has kept both of the valves in place. Scale bar, applicable to all panels, is 1 cm.

current-induced fragmentation of cold-water coral frameworks seems to be exceptional, except for occasional observations of toppled large coral colonies that had grown on unstable substrata (Wilson, 1979).

The most significant agent of colony fragmentation appears to be bioerosion (see Section 4.1, p. 109), through the mechanical abrasion or chemical corrosion of coral skeletons by a plethora of organisms. Bioerosion generates characteristic traces on skeletal remains such as grazing marks, attachment scars and excavations or borings. As these bioerosion traces are generally taxon specific, they yield valuable information for palaeontologists trying to reconstruct ancient species relationships. The net result of bioerosion is continued degradation of coral colonies and individual skeletons into smaller-sized fragments (Neumann, 1966).

The bioeroding communities of tropical shallow-water reefs have been intensely studied in terms of their composition, rates of carbonate removal and variability under different trophic regimes (e.g. Tribollet, 2008). The study of bioerosion in cold-water coral reefs is gaining momentum but quantitative data are a matter of ongoing research. A major difference between the warm-water and cold-water reef regimes is an almost complete lack of predatory bioerosion in cold, deep waters. Plagues of crown-of-thorns starfish periodically destroy corals in the Indo-Pacific (e.g. Endean, 1973). Scarid fish and some regular echinoids graze corals in search of food, thereby ingesting coral carbonate, which they excrete as faecal pellets (Steneck, 1988; Scoffin, 1992). In cold-water coral reefs, coral predators either do not exist (as in the case of the scarid fish), or are not known to occur in significant numbers. Although some coral-grazing poraniid and goniasterid asteroids have been observed, their effects on the coral remain unstudied (Krieger & Wing, 2002). Traces generated by skeleton-excavating grazers such as regular echinoids, asteroids, gastropods and chitons appear to be rare on cold-water corals (Bromley, 2005).

As cold-water coral reefs thrive in aphotic waters, the diverse photosynthetic community of endolithic cyanobacteria and algae found in shallow-water coral reefs is absent. Instead, fungi characterise the microborer community in cold-water coral frameworks (e.g. Beuck & Freiwald, 2005). Fungi use organic acids to penetrate into their calcareous substratum. The most characteristic boring fungus in aphotic corals is the chytridialid *Dodgella* that etches characteristic sac-like pits 40 µm deep into the coral skeleton (Fig. 6.8). As *Dodgella* infests the entire circumference of an exposed dead skeleton, it becomes gradually bored (micritisation). This micritised region can be seen in thin sections forming the *Dodgella*-layer (Freiwald *et al*., 1997b) and it considerably enhances intra-skeletal porosity (Wisshak, 2006), see Fig. 6.8.

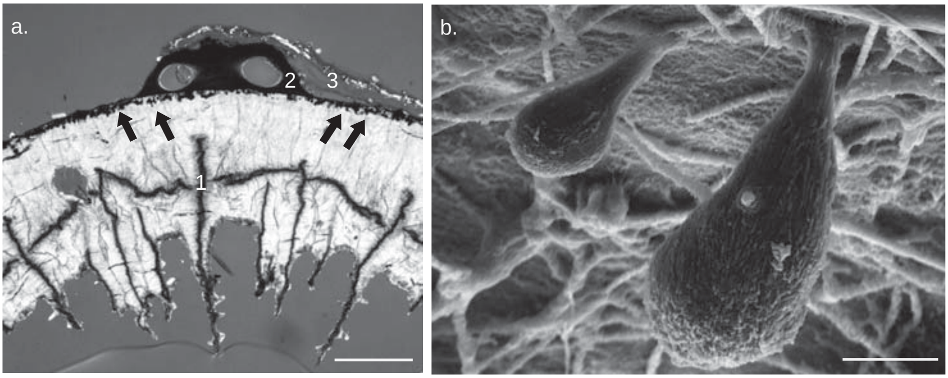


Fig. 6.8. Micro-bioerosion by the ubiquitous endolithic fungus *Dodgella*. (a) Thin section of a part of a *Lophelia pertusa* corallite (scale bar 3 mm) with the black lines representing the centres of calcification (1) in the septa and thecal wall. The '*Dodgella*-layer' made by fungal borings always follows the external circumference of infested substrata (arrowed). The coral was colonised by a spirorbid tube (2) and by a gorgonian (3), note the sclerites in the tissue. (b) Scanning electron micrograph of two cast-embedded *Dodgella* borings into a calcareous substratum highlighting the sac-shaped body and filaments of this endolithic fungus (scale bar 10 µm). Images courtesy of M. Wisshak.

In shallow-water tropical coral reefs, bivalves and sponges form very important groups of endolithic macroborers in terms of their quantitative carbonate removal. While boring bivalves are not found in cold-water coral reefs, boring sponges are the major drivers of bioerosion of coral framework in deep waters (Beuck & Freiwald, 2005). The physiology and products of excavating sponges are reviewed by Schönberg (2008). Boring sponges infest tissue-free regions of a coral skeleton but can eventually expand into the living polyp zone (Beuck *et al*., 2007). Major excavating sponge genera in cold-water coral skeletons are the haplosclerid *Aka* and the hadromerids *Alectona, Cliona, Spiroxya* and *Pione* (Calcinai *et al*., 2003; Schönberg & Beuck, 2007). The resulting trace is assigned to the ichnogenus *Entobia* (e.g. Bromley & D'Alessandro, 1984) and occurs in many ancient cold-water coral limestones (Fig. 6.9). As in shallow reef systems, boring sponges deliver large quantities of

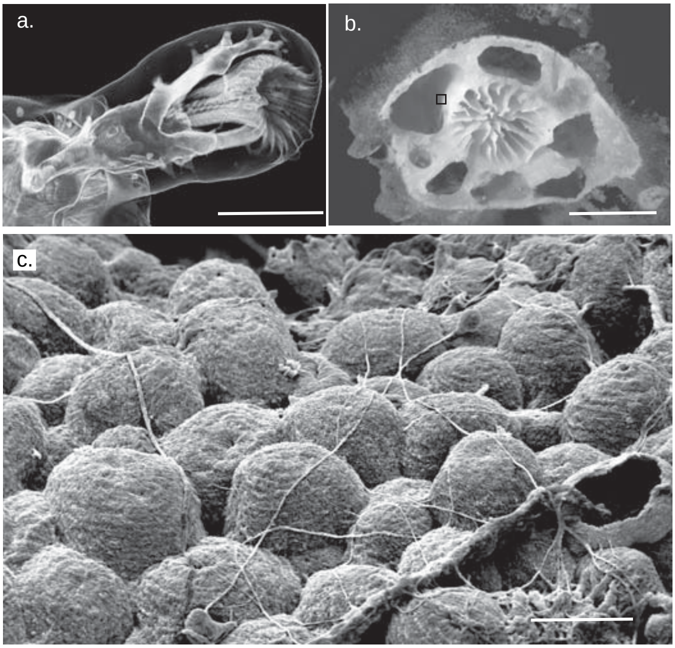


Fig. 6.9. Macro-bioerosion in *Lophelia pertusa* by boring sponges. (a) Computed tomography (CT) image of an *L. pertusa* corallite being infested by a boring sponge. The sponge expands its excavations around a live polyp. Note the sponge apertures at the outer margin of the skeleton (scale bar 1.5 cm). (b) View of sponge excavation by *Alectona millari* in a broken *L. pertusa* fragment (scale bar 0.5 cm). The rectangle marks the surface of the sponge-etching front shown in (c). (c) Scanning electron micrograph (SEM) image of cast-embedded sponge etch marks produced by *Alectona millari*. The individual loosened grains appear as 'sponge-chips' in the sedimentary environment (scale bar 100 μm). Image (a) courtesy of Siemens AG, Healthcare Sector. Image (b) reproduced from Beuck and Freiwald (2005) courtesy of Springer. Image (c) courtesy of L. Beuck.

silt-sized particles, the 'sponge chips' to the *L. pertusa* reef sedimentary environment (Freiwald & Wilson, 1998).

But the most dramatic effect of bioeroding sponges is the way they can undermine exposed coral frameworks at their bases, sometimes causing entire colonies to collapse. This destabilisation of the inner framework can modify the morphology of coral thickets and reefs by creating characteristic ring-shaped coral patches ('Wilson rings', see Section 4.1, p. 109) or creating steep flanks with overhangs as bioerosion progresses (Freiwald *et al.*, 1997a). Undermined and progressively unstable reef frameworks become increasingly vulnerable to vigorous currents, which may then enhance the breakdown process.

6.4 Preservation of the coral-associated fauna

Chapter 5 highlighted the importance of the three-dimensional coral habitat in attracting a diverse associated fauna in comparison with off-reef habitats. Faunistic studies on ancient cold-water coral thickets yield similar results (e.g. Squires, 1964; Vella, 1964; Di Geronimo *et al.*, 2005). Johnson (1964) calculated that about 70% of modern benthic marine individuals and species lack resistant hard parts and would not normally fossilise. The fossilisation potential of the coral-associated fauna also depends on the saturation state of the seawater and sediment pore water with respect to the mineralising elements and compounds (e.g. carbonate, silica) as well as the depth of the redox zone within the sediment. The fossil record is rich in genuinely preserved soft tissue organisms lacking any mineralised hard parts (Allison & Briggs, 1993) although the chemical and sedimentological requirements to prevent post-mortem soft tissue decay are rarely met in bathyal cold-water coral depositional regimes because of their vigorous currents and intense sediment bioturbation. This means that any organisms lacking mineralised hard parts will only rarely be fossilised in the sediments of a cold-water coral reef. Even possessing a carbonate shell or siliceous skeleton may not guarantee preservation; for instance, aragonite and silica are prone to early diagenetic alteration. The worst case is complete dissolution of aragonite or silica (Fig. 6.6), but more often these biominerals are replaced by the chemically more stable calcite (see Section 4.4.5, p. 130). Table 6.3 provides a qualitative overview on the fossilisation potential of the higher taxonomic categories known to occur in cold-water coral communities. We will now briefly discuss the major groups that can be found in ancient cold-water coral communities.

6.4.1 Foraminifera

Most Foraminifera secrete a calcite test, a few build aragonite tests, consist of agglutinated components or are made solely of tectin (pseudochitin) (Lipps,

Table 6.3 *Overview of the coral community (higher taxonomic levels only) with shading to give a qualitative assessment of the fossilisation potential (dark: common as fossil; grey: rare as fossil; white: exceptional as fossil) along with their hard-part mineralogies or other forms of fossilisable products (e.g. borings).*

Phylum/Class	Order/Family	Biominerals and products
Granureticulosa	Foraminiferida	mostly calcitic tests; agglutinated tests
Porifera	Hexactinellida	siliceous spicules
	Calcarea	calcitic spicules
	Demospongia	siliceous spicules; some as borings
Hydrozoa	Stylasteridae	aragonitic and rarely calcitic skeletons
Gorgonacea	Isididae	calcitic internodes and holdfasts
	Coralliidae	calcitic skeletons
Pennatulacea	Kophobelemnidae	calcitic supporting axes
Polychaeta	Eunicidae	host coral-calcified parchment tube; jaw elements
	Lumbrineridae	etch marks in host corals
	Serpulidae	calcitic or aragonitic tubes and opercula
	Spirorbidae	calcitic tubes
Sipuncula	Aspidosiphonidae	as borings
Mollusca	Polyplacophora	aragonitic valvulae; grazing marks
	Bivalvia	calcitic, aragonitic or bimineral shells; some borers
	Scaphopoda	aragonitic tubes
	Monoplacophora	aragonitic shells
	Gastropoda	mostly aragonitic shells; grazing marks
	Cephalopoda	aragonitic shells; predatory marks
Crustacea	Decapoda	calcite-chitin; calcium phosphate; carapace, claws
	Cirripedia	calcitic plates; some borings; some gall formation
	Ostracoda	calcitic valves
Echinodermata	Asteroidea	Mg-calcitic ossicles; grazing marks
	Ophiuroidea	Mg-calcitic ossicles
	Crinoidea	Mg-calcitic ossicles
	Echinoidea	Mg-calcitic ossicles; grazing marks
	Holothuroidea	Mg-calcitic ossicles
Lophophorata	Bryozoa	mostly calcitic zooecia; few as borings
	Phoronida	some as borings
	Brachiopoda	calcitic shells; pedicle etchings
Hemichordata	Pterobranchia	sclerotic tubes
Chordata	Teleostei	bones; many with otoliths
	Elasmobranchii	dermal scales; teeth

1973). A typical foraminiferal assemblage in bathyal coral sediments is dominated by imported planktonic tests (80–90%) compared with benthic Foraminifera. The latter group, however, is much more diverse. Comparative studies on the benthic foraminiferal assemblage of Late Miocene, Early Pliocene (Vella, 1964) and Late Pleistocene to Holocene (Coles *et al*., 1996; Rüggeberg *et al*., 2007) coral thicket and coral carbonate mound facies with those from the adjacent non-coral facies yield remarkable differences, again highlighting the significance of coral habitats as biodiversity hotspots. These studies show a higher species richness within the coral facies, especially within the group of epifaunally attached Foraminifera that fix themselves on the coenenchyme-free skeleton of the corals and other colonial organisms (Bednorz, 2007). The parasitic *Hyrrokkin sarcophaga* belongs to a group of epifaunal Foraminifera (see Section 5.4.1, p. 160 and Fig. 5.8) and bores into its host organism leaving a characteristic boring trace, described as *Kardopomorphos polydioryx* (Beuck *et al*., 2008), see Fig. 6.10. The

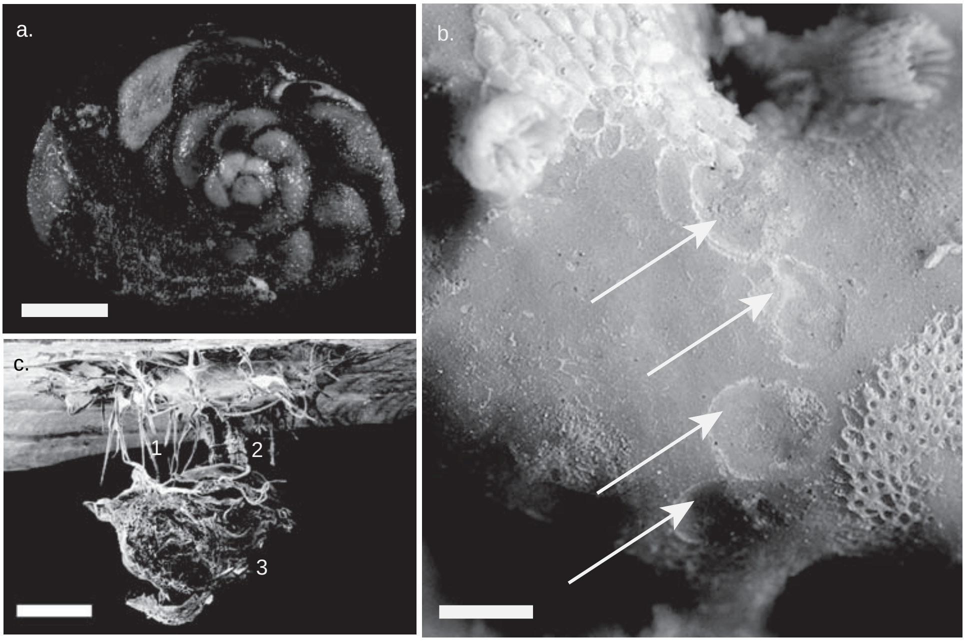


Fig. 6.10. The parasitic foraminiferan *Hyrrokkin sarcophaga* (a) generates attachment scars (arrowed in (b)) on calcareous surfaces such as a *Madrepora* coral skeleton (b). The parasitic boring trace *Kardopomorphos polydioryx* in the bivalve *Acesta excavata* is shown as a cast-embedded scanning electron micrograph (c) and consists of three parts: (1) whip-shaped filaments, (2) central boring canals and (3) the callus cast (scale bars 1 mm in (a) and (b), and 5 mm in (c)). Images (a) and (c) reproduced from Beuck *et al*. (2008) courtesy of Springer Science+Business Media. Image (b) courtesy of L. Beuck and M. López Correa.

fossil record of *Hyrrokkin* dates back at least to the Early Pleistocene of Rhodes, eastern Mediterranean (Beuck *et al.*, 2008).

6.4.2 Porifera

Sponges represent one of the most diverse phyla in cold-water coral habitats covering all size classes from sub-millimetre thin crusts, to metre-sized sponges. While the majority of sponges in cold-water coral habitats live in the dead coral framework, some seem to be associated with the living coral zone, for example in the case of *Lophelia* and *Madrepora*, the poecilosclerids *Mycale lingua, Lissodendoryx diversichela* and *Hymeraphia verticillata*, and the verongid *Hexadella dedritifera* are common (Jonsson *et al.*, 2004; Van Soest *et al.*, 2007), see Colour plates 7 and 17. Their mode of life and durable spicule materials (silica or calcite) both improve the fossilisation potential of sponges. Hexactinellids, and some families of the Demospongia, secrete amorphous biogenic silica spicules, sometimes providing them with a very dense and rigid skeleton. However, except in the polar oceans, seawater is generally undersaturated with respect to silica in the upper 1000 m, thus enhancing rapid post-mortem dissolution of silica sponge spicules (Land, 1976) and reducing their fossilisation potential. The hexactinellid sponge mounds off British Columbia are apparently growing in seawater supersaturated with silica (Conway *et al.*, 2005).

Sponges in ancient cold-water coral communities are generally rare. One hexactinellid with a rigid meshwork of silica spicules that is commonly found in modern bathyal coral habitats is *Aphrocallistes* (Conway *et al.*, 2001; Raes & Vanreusel, 2005; Henry & Roberts, 2007), see Fig. 5.5, p. 153. Its fossil record dates back to the Coniacian, Late Cretaceous (89–85 Ma) of Bornholm, Denmark (Noe-Nygaard & Surlyk, 1985), where it is preserved in deeper water, mounded chalk facies (see Fig. 6.3). This genus, together with other hexactinellids, is also found in other Late Cretaceous to Eocene deep-water chalks and limestones (Helm & Kosma, 2006; Pisera & Busquets, 2002) such as at the margins of Danian aphotic coral mounds that are rich in *Dendrophyllia* and other scleractinians in Denmark (Bernecker & Weidlich, 1990), and adjacent to the Middle Eocene *Dendrophyllia* thickets of the Ebro Basin in Spain (Fig. 6.3, Busquets *et al.*, 1994). Lithified siliceous sponges are often preserved in Pleistocene *Lophelia–Madrepora* hardgrounds in the Mediterranean Sea (Allouc, 1987; Brachert *et al.*, 1987). Calcarea secrete calcitic spicules but only those with a rigid spicule meshwork and an encrusting habit on hard substrata have fossilisation potential. For example, the minchinellid *Plectroninia* is the most abundant Calcarea genus found on dead coral framework in the Porcupine Seabight

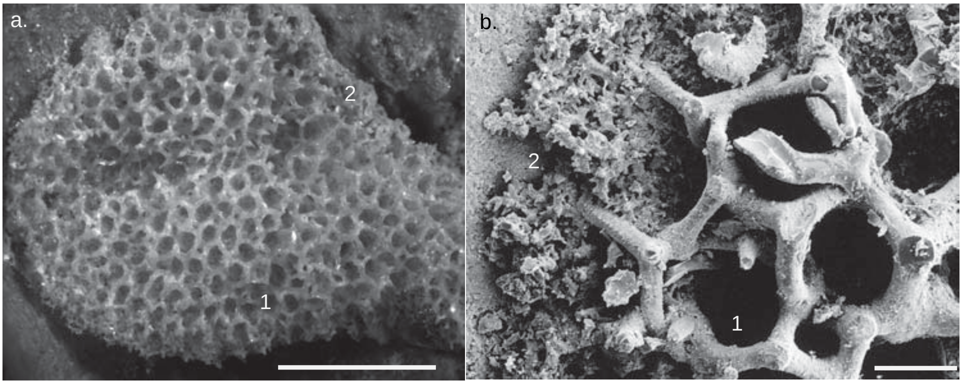


Fig. 6.11. The calcareous sponge *Plectroninia celtica* has been present in bathyal coral habitats since the Miocene. The rigid skeleton consists of regular fused honeycomb tetractines (labelled 1), fringed by a laminar layer of spiny and irregularly shaped tetractines (labelled 2). Scale bar is 1 mm in (a) and 100 µm in (b). Image (b) enlarged from an original in Könnecker and Freiwald (2005), courtesy of Springer Science+Business Media.

(Könnecker & Freiwald, 2005), see Fig. 6.11, and fossilised *Plectroninia* has been discovered in bathyal Late Miocene coral communities of Carboneras, southeast Spain (Barrier *et al.*, 1991).

6.4.3 Cnidaria

Other than the Scleractinia, cnidarians yield only occasional fossils in ancient cold-water coral assemblages. The Stylasteridae were known since the Late Cretaceous (Lindner *et al.*, 2008) and contributed nine species to coral mound formation in the Danian of Denmark (Bernecker & Weidlich, 1990; Zibrowius & Cairns, 1992), see Fig. 6.3. Gorgonacea are traditionally subdivided into two suborders: (1) Scleraxonia, with a supporting axis of magnesium calcite sclerites that are more or less fixed together by gorgonin or crystalline calcite and (2) Holaxonia, with an axis consisting of gorgonin that may be impregnated with calcium carbonate (Bayer, 1973). The sclerites of octocorals are made of magnesium calcite (Bayer & Macintyre, 2001). The oldest fossils of the scleraxonian precious coral *Corallium* were reported from the Eocene in the Pacific (Wells, 1977). The holaxonian gorgonian family Isididae (bamboo corals) appeared in the Late Cretaceous, mostly as preserved internodes and holdfasts still attached to various hard substrata in deep-water chalk facies (see Fig. 6.3 and Fig. 6.12; Voigt, 1958; Grasshoff, 1980; Malecki, 1982) and more rarely as complete specimens (Helm & Schülke, 2003). The pennatulaceans belong to the most advanced octocorals in terms of colonial complexity and functional specialisation (Bayer, 1973).

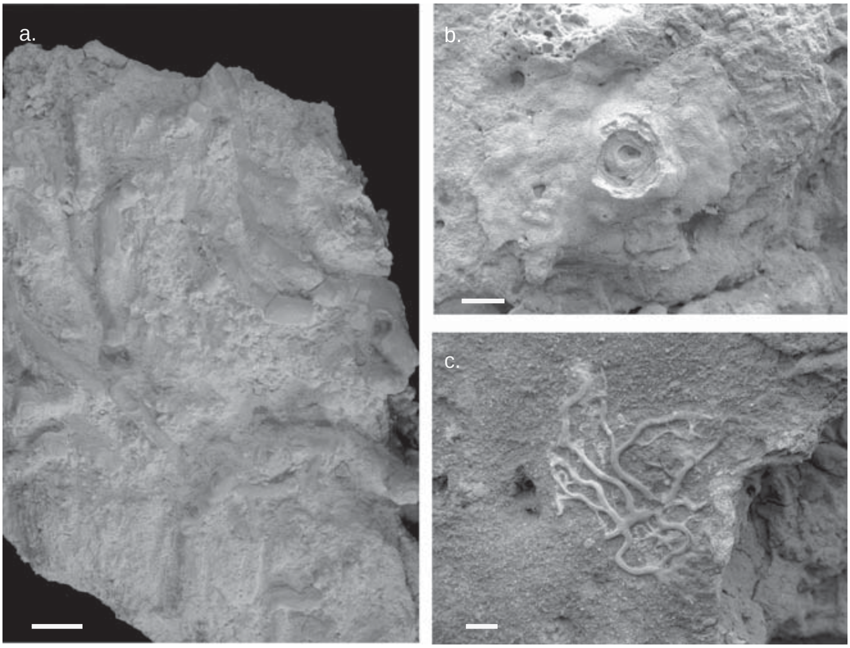


Fig. 6.12. Fossil octocorals. (a) A nearly complete *Moltkia isis* (Isididae) from the Danian coral mounds in Denmark (scale bar 1 cm). (b) Calcitic holdfast of an isidid on its hard substratum (scale bar 0.5 cm). (c) Delicate holdfast of the isidid *Keratoisis peloritana* (scale bar 1 cm). Images (b) and (c) are from Fumari on Sicily (Early Pleistocene). Image (a) courtesy of M. Bernecker. Images (b) and (c) courtesy of J. Titschack.

Some families of the pennatulaceans secrete a calcitic supporting axis known from deep-water environments since the Late Cretaceous (Voigt, 1958). Bernecker and Weidlich (2006) provide a thorough overview of octocorals from the Danian coral mounds of Fakse, including the Helioporacea, Pennatulacea, Primnoidae and Isididae (Fig. 6.12). Another stylasterid and octocoral-rich bathyal assemblage was discovered from the Late Miocene ‘red brecchia’ deposits from Carboneras, southeast Spain with isidids, primnoids, *Corallium* and colonial scleractinians such as *Madrepora* and *Dendrophyllia* (Barrier *et al*., 1991).

6.4.4 Annelida

Within the phylum Annelida, the polychaete worms represent a very diverse group in cold-water coral reefs, mirroring their high diversity in other benthic habitats. Although the ecological role of polychaetes remains largely unstudied in cold-water coral habitats, some remarkable coral–polychaete interactions are known. Some stylasterid species are infested by polynoid, spionid and syllid polychaetes (Zibrowius, 1981). The stylasterid host secretes distinct galls around the parasitic worms, which can be clearly preserved in the fossil record. The eunicid worm *Lumbrineris flabellicola* attaches and etches its membranous transparent tubes to the side of a host coral, preferably on *Caryophyllia* and *Flabellum* species, and traces of this are known since the Miocene (Zibrowius *et al.*, 1975). Several species of *Eunice* show a symbiotic relationship with scleractinians and with the stylasterid *Errina atlantica* (Winsnes, 1989; Zibrowius & Cairns, 1992), see Section 5.4.1, p. 162 and Fig. 5.10, p. 163. This intriguing relationship dates back to at least the Early Pleistocene (Titschack & Freiwald, 2005). Two more polychaete families deposit calcium carbonate as tubes firmly attached to the coral skeleton: (1) the Serpulidae and (2) the Spirorbidae, both known in the fossil record since the Palaeozoic. The Plio-Pleistocene serpulids of Mediterranean bathyal coral communities were studied by Zibrowius (1987) and Di Geronimo *et al.* (2005).

6.4.5 Mollusca

Shelly molluscs probably yield the most important macrofossils in ancient cold-water coral deposits. Compared to coarse neritic and coastal sediment sequences, the prevalence of hemipelagic to pelagic mud and siltstones helped preserve even tiny and fragile aragonitic remains. This holds especially true for the mostly aragonite shells of gastropods such as those from the Danian coral limestones (e.g. Ingemann Schnetler & Petit, 2006), the Late Miocene to Pliocene *Lophelia* thickets (Squires, 1964; Beu, 1967) and the Early Pleistocene Sicilian *Lophelia–Madrepora* limestones (Di Geronimo *et al.*, 2005).

In bathyal coral habitats, the majority of symbiotic gastropods are thought to be predators or parasites (Buhl-Mortensen & Mortensen, 2004c), although these relationships have yet to be documented. Sponge-eating fissurellids are often found in both fossil and modern cold-water coral gastropod assemblages. Some species are thought to show close, if not even obligate, associations with cold-water corals. A striking example is the trochid *Calliostoma maurolici*, which has been observed grazing on coral soft tissue (Beck & Freiwald, 2006), see Fig. 6.13. This species is known from Early Pleistocene bathyal coral communities in Sicily (Di Geronimo *et al.*, 2005). Most epitoniids are ectoparasitic suctorial carnivores on cnidarians like *Iphitus tuberatus* from the Pleistocene of the Mediterranean and Recent northeast Atlantic *Lophelia–Madrepora* (Fig. 6.13), and *Iphitus neozelandica* from *Goniocorella* thickets in the southwest Pacific (Beu, 1978; Taviani & Sabelli, 1982; Beck & Freiwald, 2006). Among the Muricoidea, the coralliophilids live as ectoparasites on cnidarians including scleractinians (Oliverio & Gofas, 2006). As discussed in Section 5.4.1 (p. 161) the

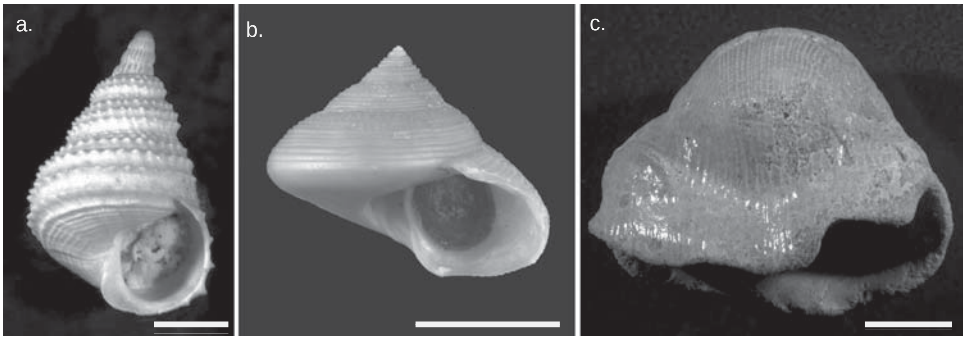


Fig. 6.13. Bathyal coral-parasitising gastropods. (a) *Iphitus tuberatus* (Recent, scale bar 1 cm). (b) *Calliostoma maurolici* (Recent, scale bar 1 cm). (c) *Pedicularia sicula* (Pleistocene, scale bar 2 mm). Images courtesy of T. Beck.

ovulid *Pedicularia* is an obligate parasite in some stylasterids (Arnaud & Zibrowius, 1979; Goud & Hoeksema, 2001), see Fig. 6.13. The parasitic gastropod and cold-water coral relationship dates back to at least the Late Eocene (37–33 Ma), when a *Pedicularia*–stylasterid assemblage was described from Eua Island in the Pacific (Ladd, 1970). Probably the oldest findings of *Coralliophila* and *Iphitus* in bathyal coral communities come from the Late Miocene of Carboneras, southeast Spain, an outcrop rich in stylasterids, octocorals and solitary and colonial scleractinians (Barrier *et al*., 1991).

Bivalves are remarkably common in both the living and dead zone of cold-water coral frameworks with byssally attached and cemented species being particularly abundant. One of the largest bivalves found in coral habitats worldwide is the limid file clam *Acesta* (López Correa *et al*., 2005). The byssally attached *Acesta excavata* lives in dense populations preferably on steeply inclined dead coral framework, from where the shells fall to the seabed after death and accumulate as shell plasters. The *Acesta* shell is also often infested by the parasitic foraminifer *Hyrrokkin sarcophaga* (Beuck *et al*., 2008), see Section 5.4.1, p. 160, Section 6.4.1, p. 200 and Fig. 6.10. Deep-sea oyster aggregations formed by a new *Neopycnodonte* species can form an unusual bivalve facies, often associated with Late Pleistocene *Lophelia–Madrepora* occurrences. *Neopycnodonte* grew on vertical canyon cliffs in the Mediterranean and individual oysters reached sizes of up to 30 cm. This species was recently found alive in the bathyal zone on the Azores (Wisshak *et al*., 2008), see Fig. 6.14.

6.4.6 Crustacea

Among the diverse group of crustaceans only few have a fossilisation potential. The decapods have calcite-impregnated hard parts that rapidly disintegrate after

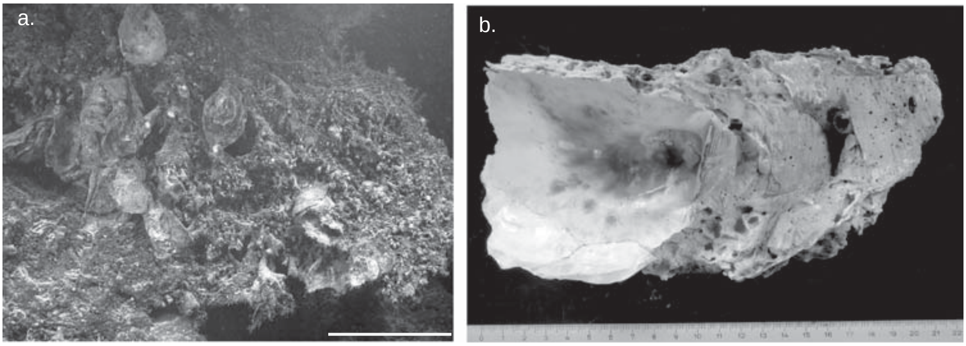


Fig. 6.14. (a) Deep-sea oyster aggregations of *Neopycnodonte* cemented on Late Pleistocene *Lophelia* framework, lithified in place on an escarpment at 683 m water depth near Linosa, Strait of Sicily (scale bar 50 cm). (b) Recent deep-sea *Neopycnodonte* from the Azores. Image (a) courtesy of MARUM-QUEST ROV, Bremen. Image (b) courtesy of M. Wisshak.

death. In fossil cold-water coral settings decapods are mostly incomplete with a preferred preservation of the carapace and claws as seen in the extinct decapod *Dromiopsis* and remains of galatheid squat lobsters from the Danian coral mounds (Jakobsen, 2003) and from the Early Pleistocene of Rhodes (Titschack & Freiwald, 2005). Important present-day decapod genera such as *Galathea* and *Munida* were present in Danian (65–61 Ma) cold-water coral mounds (Jakobsen, 2003). The remaining eumalacostracan crustaceans have weakly calcified or non-calcified hard parts and therefore a poor fossil record.

One crustacean lineage, the Cirripedia, turned to sessile lifestyles: the pedunculate lepadids and various barnacles (balanids and verrucids) and the Acrothoracica and Ascothoracica, which live as parasites on molluscs, echinoderms and cnidarians (Newman *et al*., 1969). However, the balanomorph and verrucomorph barnacles are more common in cold-water coral habitats where they settle on both dead scleractinian frameworks and octocorals. Their calcitic plates can form important components of the sediment in current-swept gullies such as those in the Belgica mounds province in the Porcupine Seabight, northeast Atlantic (e.g. Foubert *et al*., 2005). The endoparasitic ascothoracid–coral relationship has existed since the Late Cretaceous. The internodes of the isidid octocoral *Moltkia minuta* were apparently often infested by the ascothoracid *Endosacculus moltkiae* (Voigt, 1959) with the isidid secreting one or more spherical galls around the entombed parasites. Petracid and lithoglyptid ascothoracids may also stimulate gall formation in *Lophelia* and *Enallopsammia* (Grygier, 1982, 1990; Grygier & Newman, 1985).

Ostracods secrete a calcitic double valve thus making them an important microfossil group. But despite their high fossilisation potential and common occurrence in fossil bathyal coral sites, they are not often reported. Exceptions are the studies of Coles *et al*. (1996) and Di Geronimo *et al*. (2005) from Pleistocene *Lophelia–Madrepora* deposits.

6.4.7 Echinodermata

Echinoderms are a very common group in deep-sea environments and all classes of echinoderms are present in cold-water coral reefs. They have complex skeletons with magnesium-calcite mineralogy. Asteroids and ophiuroids have a skeleton consisting of numerous discrete ossicles of various shapes held together by muscles and ligaments that rapidly disintegrate after death. The same post-mortem fate is experienced by crinoids and the (reduced) holothurian skeletons. Therefore, complete asteroids, ophiuroids and crinoids are extremely rare but their durable ossicles form common components in cold-water coral sediments. Probably the best documentation of echinoderms in ancient deeper water coral mounds comes from the Danian coral facies with well preserved crinoids (Nielsen, 1913; Donovan & Jakobsen, 2004) and echinoids (e.g. Brotzen, 1959). Roux *et al*. (1988) described remains of the stalked crinoid *Diplocinus wyvillethomsoni* from Early to Middle Pleistocene bathyal coral assemblages in the Messina Strait area. Stalked crinoids became extinct in the Mediterranean Basin after the Middle Pleistocene.

6.4.8 Bryozoa

Bryozoa are also common constituents of cold-water coral communities (Pulpeiro *et al*., 1988; Zabala *et al*., 1993). In general, the rooted, erect cellariiform bryozoans are confined to soft substrata whereas encrusting growth forms prevail on the coral framework. The majority are cyclostomes and cheilostomes. The weakly calcified ctenostomes are only represented as bioerosive endolithic species (Pohowsky, 1978), which also occurred in Danian coral mounds (Boekschoten, 1970) and stratigraphically younger bathyal coral assemblages (Beuck & Freiwald, 2005). Erect and encrusting cyclostome and cheilostome bryozoans from Early Pleistocene *Lophelia* assemblages in Sicily (Di Geronimo *et al*., 2005) and Rhodes (Moissette & Spjeldnaes, 1995) are common constituents of the coral facies. In the Danish Basin, coral mound formation in the Middle Danian was preceded by bryozoan mound formation from Late Cretaceous to Early Danian age (Surlyk, 1997). The delicate branching bryozoans grew in place and baffled pelagic and detrital benthic carbonate mud over time to build 5–11 m high skeletal mound structures under a gentle current regime (Bjerager & Surlyk, 2007a, 2007b).

6.4.9 Other groups

Brachiopods are commonly encountered in ancient bathyal coral sediments from the Danian period onward. In the Danian coral limestones some species, such as *Rhynchonella flustracea*, were specifically adapted to fit between the colony branches of *Dendrophyllia candelabrum* (Asgaard, 1968). Hard substrata-cementing brachiopods like *Crania* can be expected in such a palaeoenvironment. However, brachiopod traces are more common, including pits etched on coral skeletons by the pedicle of articulate brachiopods (Bromley & Surlyk, 1973). The resulting trace fossil, *Podichnus*, is known from both Early Pleistocene (Bromley, 2005) and modern *Lophelia* skeletons (Wisshak *et al*., 2005).

Recent coral habitats may support a diverse, even characteristic, fish community (see Section 5.5, p. 163), which can be targeted as a commercial fishery. Indeed bottom trawl fishing in cold-water coral habitats has raised concerns over the sustainability of such fisheries (see Section 8.1.1, p. 237). Cartilaginous fish (Chondrichthyes) such as sharks, skates and rays lack true bones. Only the sharp teeth and occasional calcified vertebrae may survive as fossils in the rock record. Fossil remains of fish preserved in ancient cold-water coral facies seem to be rare, as are scientific studies in this field. Bernecker and Weidlich (2005) briefly mentioned shark teeth from several species in the Danian coral mounds of Fakse in Denmark. Teleost fish have much better fossilisation potential because of their bony skeleton. Most important, however, are the tiny otoliths ('ear bones') of teleost fish, which can be found in a broad spectrum of sedimentary facies. Otoliths consist of aragonite and show clear growth zones, sometimes even at daily resolution (Pannella, 1971). In this way, the entire lifetime of a fish is locked as a geochemical record in the otolith, thus being a very useful tool to reconstruct fish migration or palaeoclimatic conditions (e.g. Høie *et al*., 2004). Otoliths may even allow precise species-level taxonomic identifications in Cenozoic sediments (Nolf, 1995). Because aragonite is better preserved in muddy pelagic deposits, otoliths are common constituents in bathyal sediments. Indeed prevalent myctophid and macrourid otoliths are an indicator of bathyal conditions (Nolf, 1995) and this has been found by preliminary otolith studies in Early Pleistocene cold-water coral communities from Grammichele, Sicily (Di Geronimo, 1979) and from Late Pleistocene communities from a coral carbonate mound in the Porcupine Seabight (Heindel, 2004). A thorough review of bathyal Mediterranean otoliths, changes in composition and palaeoclimatic trends was compiled by Girone *et al*. (2006).

This chapter provides an overview of when cold-water coral communities evolved in the Mesozoic to Early Cenozoic and has highlighted selected aspects of the taphonomy and palaeontology of the associated fauna. Cold-water coral habitats, particularly those formed by the reef framework-forming scleractinians, seem to have expanded through their present-day geographic distribution along the continental margins worldwide over the last 2–3 million years. Interestingly, many of the coral–symbiont relationships reported probably developed in the bathyal zone within this geologically short time span. If this can be substantiated by further research, cold-water coral habitats may be recognised as a major evolutionary centre in the deep sea. Our next chapter considers how the fossil and more recent remains of cold-water corals have helped open a window back into the periods of the Earth's history when these corals were alive.

7

Corals as archives

> *Corals are diaries that record within their pages many types of environmental information . . .*
>
> Geochemistry of corals: proxies of past ocean chemistry,
> ocean circulation, and climate
> Ellen R. M. Druffel (1997)

Viewed from space the oceans dominate the surface of the Earth – as Arthur C. Clarke once noted, 'How inappropriate to call this planet Earth when it is quite clearly Ocean.' In terms of climate, the oceans are the Earth's major heat storage and transport system. For example, the first three metres of the oceans alone have an equivalent heat capacity to the Earth's entire atmosphere. Ultimately it is the oceans that exert the strongest control over planetary climate change and so perhaps it is not surprising that the clues to past climate change and the symptoms of future climate change can be found in the ocean record. Palaeoceanographers have reconstructed past climatic conditions using marine temperature proxies recorded in diverse sources ranging from foraminiferal tests in deep-sea sediments to annually banded shallow-water tropical corals. For example, oxygen isotope records from shallow, warm-water corals have revealed a recent, long-term warming and/or freshening throughout tropical regions (see review by Grottoli & Eakin, 2007). As predicted by Druffel (1997), cold-water corals are now emerging as a key archive of intermediate water-mass history. Unlike sediment-based foraminiferal records, which can be disrupted by the sediment mixing activity of infauna (bioturbation), coral skeletons offer continuous, high-resolution archives. Unlike tropical corals they are not restricted to the shallow, euphotic zone at tropical latitudes. Since individual cold-water corals may live for hundreds to thousands of years (Section 3.4.2, p. 91) and their reefs and mounds may accumulate for tens to even millions of years (see Case study 4.1, p. 122) cold-water corals offer unparalleled long-term ocean climate records where other high-resolution archives are scarce.

7.1 Biomineralisation

The vast majority of calcium carbonate production is biologically mediated, and this biocalcification is usually referred to simply as calcification. Calcification appears to have first evolved at the start of the Cambrian period (540 Ma) and is of fundamental importance in both planktonic (e.g. foraminiferans, coccolithophores, pteropods) and benthic (e.g. molluscs, echinoderms, corals, calcareous algae) organisms that use calcified structures for many purposes among which protection and anchoring to substrata are clearly important to corals. At the growing tips of skeletal structures the so-called centres of calcification (also referred to as early mineralisation zones, crystal nucleation regions and centres of rapid accretion) are laid down first. These are subsequently overgrown by longer, fibrous aragonite crystals, usually in a series of discrete, identifiable layers. For more information on coral biomineralisation see Cuif and Dauphin (2005b) or reviews by Cohen and McConnaughey (2003) and Allemand *et al*. (2004).

7.1.1 Coral calcification

Studies of calcification in cold-water corals have only recently begun and even though zooxanthellate reef-building coral calcification has been the subject of intense study for many years, the mechanisms underlying zooxanthellate coral calcification remain hotly debated. Two broad schools of thought on coral calcification have emerged. The ‘physicochemical school’ (Constantz, 1986) proposes that calcification takes place in the space (extracellular calcifying fluid) beneath calicoblastic cells of the coral’s ectoderm via mechanisms similar to those during the growth of abiotic aragonite cements (Constantz, 1986), see Cohen and McConnaughey (2003) for a review. On the other hand, the ‘organic matrix school’ proposes that calcification is mediated via an organic matrix secreted by the coral (see Allemand *et al*., 1998; Tambutté *et al*., 2007b).

The earliest studies in the first half of the twentieth century noted that zooxanthellate coral calcification was fastest in the light, promoting a rich vein of research exploring the relationship between zooxanthellae photosynthesis and coral calcification. The reef framework-forming corals described in this book are from deep, dark waters and do not contain zooxanthellae, but because the vast majority of studies have been made on shallow-water zooxanthellate species these will be summarised here to indicate the state of current research on coral calcification. Research on cold-water coral calcification should be a high priority for several reasons: (1) without endosymbiotic zooxanthellae and the effects of photosynthesis, studying the mode of coral calcification may be more tractable; (2) knowledge of the calcification mechanism will aid interpreting isotopic fractionation caused by coral ‘vital effects’ (see Section 7.1.2 below); and (3) mechanistic understanding of calcification is essential to develop predictions of the effects of ocean acidification and forecast the points at which coral calcification and growth may tip across to states of dissolution and framework erosion (see Section 8.1.4, p. 247).

A coral’s skeleton is extracellular and produced by individual polyps each forming a bag-like structure with walls composed of just two cell layers separated by a gelatinous mesoglea (Sections 3.1, p. 68 and 3.5, p. 94). The single outer cell layer (ectoderm or epidermis) facing the seawater is known as the oral ectoderm. Moving inwards, this is followed by the mesoglea and the inner cell layer (endoderm or gastrodermis), termed the oral endoderm. Each coral polyp encloses a space, the coelenteron, with one opening to the surrounding seawater. This opening functions as both mouth for feeding and anus to void any solid wastes, and allows water exchange between the internal coelenteric cavity and seawater. The mouth is surrounded by tentacles either in multiples of six in the Hexacorallia or eight in the Octocorallia. At the base of the polyp the same pattern of cell layers is repeated giving an inner cell layer (endoderm or gastrodermis), the aboral endodermis that faces the coelenteron, followed by the mesoglea and an outer cell layer that directly faces the skeleton. This aboral ectoderm layer is typically flat with few, if any, cnidocytes and is known as the calicoblastic epithelium. Calicoblastic cells in this layer contain many mitochondria implying an energy-demanding role (Allemand *et al.*, 2004) and it is this tissue that calcifies producing the coral’s skeleton (Fig. 7.1).

For biomineralisation to take place there must be simultaneous supply of ions (Ca^{2+} and dissolved inorganic carbon) and perhaps also an organic matrix present to provide a framework for skeletogenesis or seeds for crystal formation, although the role and importance of the organic framework in coral calcification is poorly understood (Cohen & McConnaughey, 2003; Tambutté *et al.*, 2007b). Calcium transport could be between cells (paracellular), via passive diffusion dependent on an electrochemical gradient, or through cells (transcellular) so requiring energy and specific carrier proteins to cross cell membranes. Incorporation of radioactive ^{45}Ca into the skeleton of the zooxanthellate coral *Stylophora pistillata* within 2–4 minutes implies rapid and efficient carrier-mediated transport rather than passive diffusion, and pharmacological studies suggest these transport proteins are located on the calicoblastic epithelium (Tambutté *et al.*, 1996). But for calcification to take place the protons produced when Ca^{2+} and HCO_3^- are combined to form calcium carbonate must be removed from the site of calcification. McConnaughey (1991) hypothesised that this was achieved by $Ca^{2+}/2H^+$ exchange via a Ca^{2+}-ATPase mediated exchanger (Zoccola *et al.*, 2004). However, this large proton flux through the aboral cell layers would

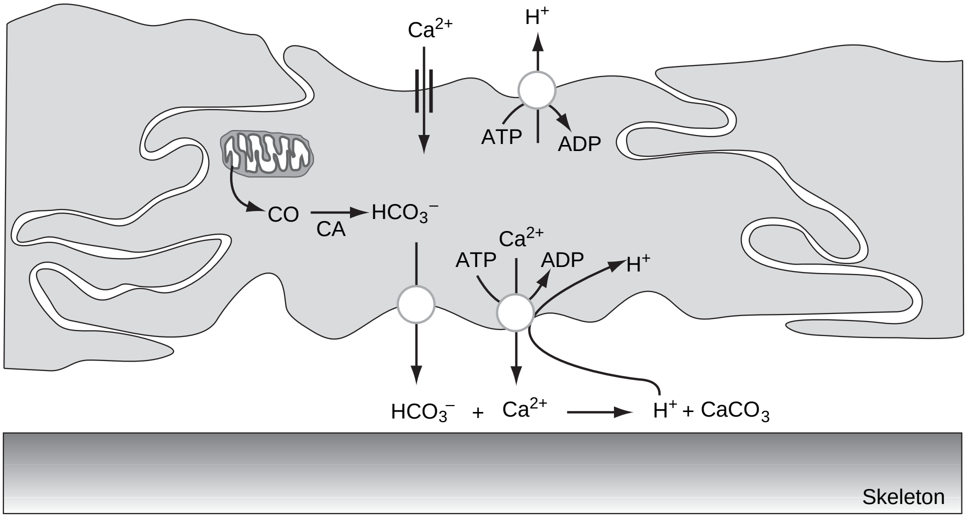


Fig. 7.1. Schematic diagram illustrating possible pathways of calcium and dissolved inorganic carbon transport through calicoblastic cells during calcification of a scleractinian coral, see text for details. Figure reproduced from Allemand *et al.* (2004) with permission of Elsevier.

greatly perturb intracellular pH. If Ca^{2+} and protons are exchanged in this way there is at present no explanation for how intracellular pH is maintained (Gattuso *et al.*, 1999).

Dissolved inorganic carbon (DIC) supply to the site of calcification is necessarily more complex than calcium supply because DIC forms interconvertable charged ionic species (HCO_3^- and CO_3^{2-}), requiring active carrier mechanisms as well as dissolved, freely diffusing carbon dioxide. These are all potentially supplied from ambient seawater or metabolically respired CO_2, or a combination of the two, and persist under pH-dependent equilibria (see Topic box 7.1). Since DIC contributes both to calcification and photosynthesis it has proved hard to disentangle these processes in zooxanthellate corals but recent progress has been made. Double-labelling studies by Furla *et al.* (2000) using ^{45}Ca and $H^{14}CO_3$ have shown that ^{14}C is incorporated in the skeleton of *Stylophora pistillata* at a lower rate than ^{45}Ca implying that the inorganic ^{14}C label in the external seawater is considerably diluted by another source of inorganic carbon, likely to be metabolically respired CO_2 as suggested by earlier work (Goreau, 1961; Pearse, 1970; Erez, 1978). The high density of mitochondria in calicoblastic cells indicates a significant capacity to produce respired CO_2 and respiration rates of *S. pistillata* confirm that this coral could meet its calcification DIC demands from respired CO_2 (Furla *et al.*, 2000). On balance, Furla *et al.* estimated that 70–75% of the DIC needed for calcification in *S. pistillata* was supplied by respired CO_2.

Topic box 7.1 **Seawater carbonate chemistry**

Understanding the carbonate chemistry of seawater is essential to those studying cold-water corals for two reasons. Firstly, carbonate chemistry determines whether or not it is physically possible for organisms, such as corals, to calcify and a basic understanding of this chemistry is essential to interpret potential calcification mechanisms. Secondly, as the effect of anthropogenic carbon dioxide release on global temperatures becomes apparent, there is growing awareness that this CO_2 is also perturbing the chemistry of the oceans, driving down pH and causing ocean 'acidification' (see discussion of ocean acidification in Section 8.1.4, p. 247). Here we briefly summarise important aspects of this chemistry and refer the reader to Stumm and Morgan (1996), Gattuso *et al.* (1999), the Royal Society (2005), Kleypas *et al.* (2006), Zeebe and Gattuso (2006) and Barker (2007) for more detailed information.

Two constituents of seawater allow marine organisms to calcify, calcium ions and dissolved inorganic carbon:

$$Ca^{2+} + 2HCO_3^{-} \leftrightarrow CaCO_3 + CO_2 + H_2O \qquad \text{(Eq. 7.1)}$$

$$Ca^{2+} + CO_3^{2-} \leftrightarrow CaCO_3 \qquad \text{(Eq. 7.2)}$$

Calcium is primarily available as divalent ions (Ca^{2+}), but **dissolved inorganic carbon** or DIC (also known as ΣCO_2, TCO_2 and C_T) in seawater takes three forms controlled by more complex chemical equilibria. These are: (1) dissolved carbon dioxide and carbonic acid (CO_2 and H_2CO_3, usually denoted simply as CO_2), (2) bicarbonate ions (HCO_3^{-}) and (3) carbonate ions (CO_3^{2-}). These exist in equilibria that depend upon temperature, salinity and pressure and critically upon pH ($-\log_{10}[H^+]$), see Fig. 7.2.

$$CO_2 + H_2O \leftrightarrow H_2CO_3 \leftrightarrow HCO_3^{-} + H^+ \leftrightarrow CO_3^{2-} + 2H^+ \qquad \text{(Eq. 7.3)}$$

The **total alkalinity** (A_T) of seawater is effectively its ability to neutralise a strong acid; more precisely A_T is the concentration of all bases in the seawater that can accept protons. The greatest proportion of seawater A_T derives from carbonate and bicarbonate ions. The level of alkalinity indicates the buffering capacity of the seawater to additional protons that would lower pH promoting acidification.

The calcium carbonate saturation state (Ω) of seawater is:

$$\Omega = [Ca^{2+}][CO_3^{2-}]/K^*_{sp} \qquad \text{(Eq. 7.4)}$$

Where $[Ca^{2+}]$ and $[CO_3^{2-}]$ are the concentrations of calcium and carbonate ions respectively and K^*_{sp} is the stoichiometric solubility product. Since the solubility of calcium carbonate depends on mineral form, calcite and aragonite have differing

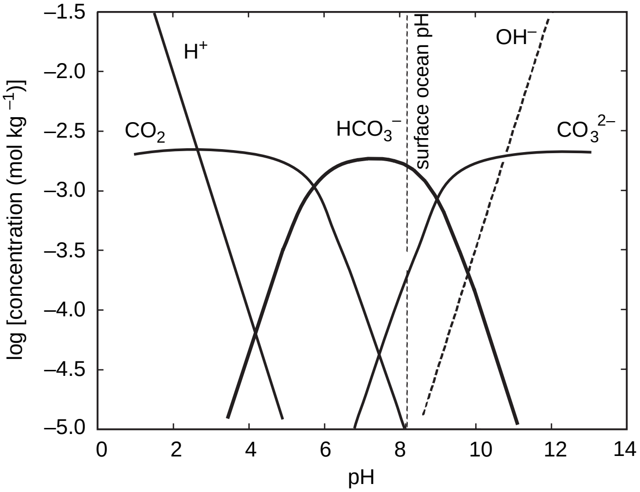


Fig. 7.2. Bjerrum plot showing typical concentrations of dissolved carbonate species in seawater as a function of pH. Figure redrawn from Zeebe and Gattuso (2006).

saturation states (aragonite being the more soluble). When $\Omega = 1$, the system is at equilibrium, and when $\Omega < 1$ the seawater is undersaturated with respect to carbonate and the equilibrium will shift toward dissolution. The solubility of calcium carbonate increases with pressure (water depth) and thus there is a depth or horizon in the oceans where calcium carbonate will begin to dissolve (the lysocline). Since aragonite is the more soluble, the aragonite saturation horizon is shallower than that for calcite. The implications of anthropogenic CO_2 on saturation state are discussed in Section 8.1.4, p. 247.

Although calcification actually *produces* CO_2 (see Equation 7.1 above) it is important to note that in typical surface ocean conditions, CO_2 concentration only increases by ~0.3 mole per mole $CaCO_3$ precipitated (DIC = 2000 μmol kg^{-1}, pH = 8.2, T = 15°C, S = 35 psu). To calcify, a coral needs to bring both calcium and DIC constituents together under equilibrium conditions favouring calcium carbonate deposition and to eliminate the protons produced (see Section 7.1.1, p. 212). At the typical surface pH of seawater (8.2), 89% of DIC is bicarbonate (HCO_3^-), 10.5% is carbonate (CO_3^{2-}) and 0.5% is carbon dioxide (CO_2). It is important to note that atmospheric pCO$_2$ and temperature have opposite, but not equal, effects on aragonite saturation state. Increasing concentrations of dissolved CO_2 *decrease* carbonate concentration and aragonite saturation state whereas increasing temperatures *increase* aragonite saturation state, but only slightly (Fig. 7.3).

The **hydration and hydroxylation of carbon dioxide** and water are also important reactions, especially to understand models of 'vital effects' in carbon and oxygen isotopic abundance in cold-water coral skeletons (see Section 7.1.2, p. 218):

Topic box 7.1 (cont.)

1. Hydration

$$CO_2 + H_2O \leftrightarrow HCO_3^- + H^+ \qquad \text{(Eq. 7.5)}$$

2. Hydroxylation

$$CO_2 + OH^- \leftrightarrow HCO_3^- \qquad \text{(Eq. 7.6)}$$

These reactions are slow to equilibrate, unless catalysed by carbonic anhydrase (see Section 7.1.1, p. 217).

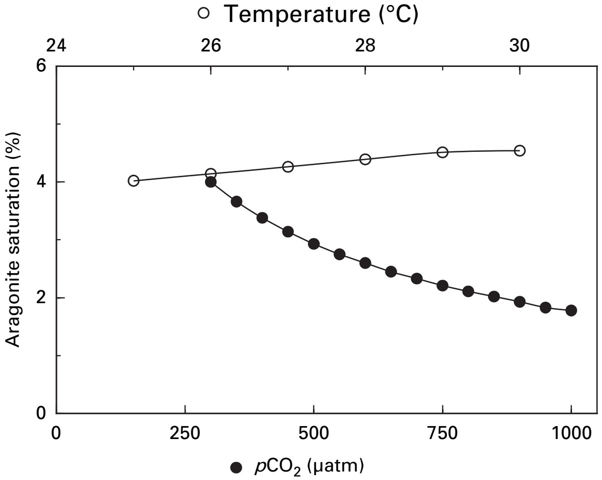


Fig. 7.3. Increased pCO_2 and temperature have opposite effects on the aragonite saturation state of seawater. Closed circles show saturation state as a function of pCO_2 (salinity = 35 psu; total alkalinity = 2350 µeq kg^{-1}; temperature = 25°C). Open circles show saturation state as a function of temperature (salinity = 35 psu; total alkalinity = 2350 µeq kg^{-1}; pCO_2 = 600 µatm). Figure reproduced from Gattuso *et al.* (1999) with permission of the American Society of Zoologists.

The azooxanthellate precious gorgonian coral *Corallium rubrum* also appears to derive most of the DIC it needs for calcifying its sclerites and axial skeleton from respired CO_2 (Allemand & Grillo, 1992). However, it seems that the importance of respired CO_2 as a source of DIC for coral calcification may vary between species and/or environmental settings. Lucas and Knapp (1997) found that the major source of DIC for sclerite calcification in the gorgonian *Leptogorgia virgulata* was respired CO_2 followed by bicarbonate. Adkins *et al.* (2003) in their study of stable carbon and oxygen isotopes found that there was little evidence

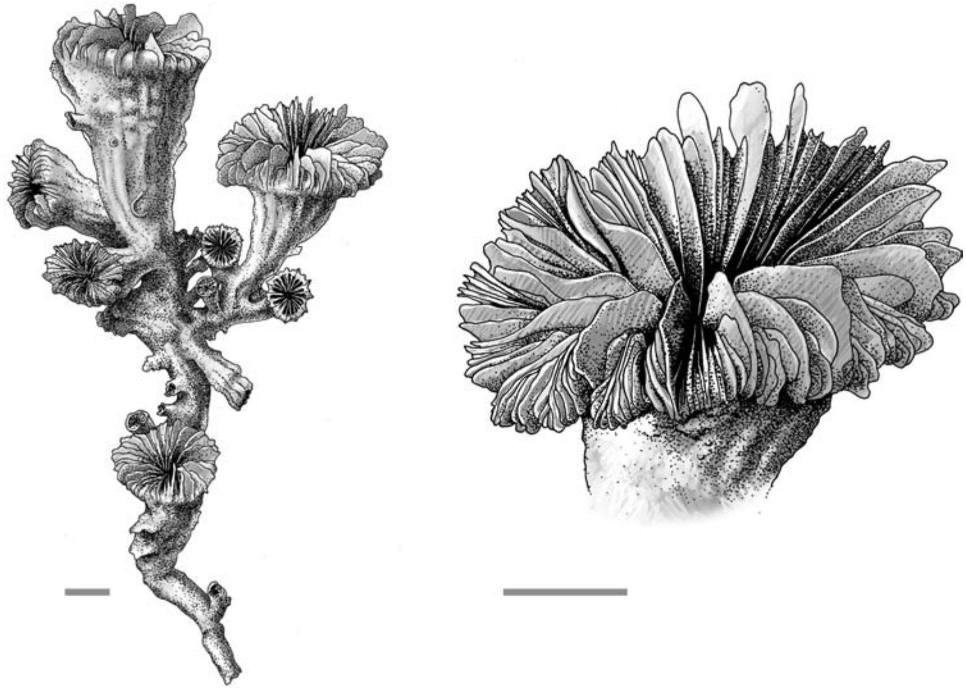


Fig. 7.4. Drawing of the scleractinian coral *Desmophyllum dianthus* with detail showing the septal structure within a coral calyx. When these solitary corals reproduce, they often attach to the parent corallum forming a strong pseudocolony. This large, slow-growing and ubiquitous species has been used in many palaeoceanographic studies. Both scale bars 10 mm.

for respired CO_2 in skeletons of the cold-water coral *Desmophyllum cristagalli* (= *D. dianthus*, see Fig. 7.4) whereas *Lophelia pertusa* skeletons appeared to incorporate a significant amount of respired carbon.

The final part of this jigsaw involves the enzyme carbonic anhydrase (CA), long implicated in coral calcification (Goreau, 1959). Carbonic anhydrase catalyses the interconversion between carbon dioxide and bicarbonate:

$$CO_2 + H_2O \leftrightarrow HCO_3^- + H^+ \qquad \text{(Eq. 7.7)}$$

thus converting metabolically produced carbon dioxide to bicarbonate that is then available for calcification. Carbonic anhydrase has been located histochemically in the calicoblastic epithelium of *Acropora hebes* (Isa & Yamazato, 1984) and when it was permanently inhibited with ethoxyzolamide, calcification rates in *S. pistillata* were reduced by 80% (Allemand *et al.*, 2004 quoting Tambutté *et al.*, 1996). Recent work on the azooxanthellate coral *Tubastraea aurea* also shows that CA inhibition reduces calcification and that this enzyme is present in organic matrix proteins synthesised by the calcifying tissues implying that, as well as providing structural organisation, the organic matrix may also assist in catalysing DIC conversion at the site of calcification (Tambutté *et al.*, 2007c).

On balance, the process of coral calcification may be summarised as follows. The coral effectively creates a supersaturated solution beneath its calicoblastic epithelium by exchanging two protons for each Ca^{2+} ion (membrane-bound Ca^{2+}-ATPase ion carrier). Since protons are removed, the pH of the fluid between the calicoblastic epithelium and the skeleton increases promoting carbonate ion (${CO_3}^{2-}$) formation. Under these conditions of heightened calcium and carbonate ion concentration, calcium carbonate precipitates from solution either nucleated on an organic matrix or perhaps directly onto the existing skeleton. Carbon dioxide continually diffuses through the calicoblastic epithelial cells into the calcifying region to replenish dissolved inorganic carbon at the site of calcification. The nature of the calcifying region is uncertain, with vigorous debate over the role of an extracellular calcifying space versus a compartmentalised calicoblastic cell layer, see below.

7.1.2 Vital effects

If calcium carbonate is allowed to precipitate slowly from solution, the division of stable carbon (^{12}C,^{13}C) and oxygen (^{16}O,^{18}O) isotopes between the solution and the crystallised $CaCO_3$ will be determined thermodynamically, and these isotopes will be incorporated in equilibrium. However, in biological calcification these isotopes are frequently not partitioned in equilibrium and show ‘vital effects’ as distinctive offsets from equilibrium (Weber & Woodhead, 1972). These vital effects vary from some organisms that calcify in near equilibrium with surrounding water (e.g. bivalve molluscs) to others, including cold-water azooxanthellate corals (Emiliani *et al.*, 1978), that show variable levels of disequilibrium. In the case of cold-water scleractinian corals this manifests as a strong linear correlation between $\delta^{18}O$ and $\delta^{13}C$ (Fig. 7.5) whereby $\delta^{18}O$ may be depleted by up to 5‰ and $\delta^{13}C$ by up to 15‰ from equilibrium (Sherwood & Risk, 2007). Similar strongly correlated relationships between $\delta^{18}O$ and $\delta^{13}C$ were seen in the cold-water calcitic gorgonian *Corallium niobe* (Druffel *et al.*, 1990). Over the last 50 years, oxygen isotope variations have become a standard geochemical tool for reconstructing past seawater temperatures so a great deal of effort has gone into trying to understand these vital effects in coral calcification. Oxygen isotopes also vary with salinity but since cold-water corals are found in very constant salinities this relationship will not be discussed in further detail. More recently, concern over anthropogenic climate change has accelerated palaeotemperature proxy research and driven a rapidly developing body of work on coral geochemistry and biomineralisation. Here we summarise some of the issues that have emerged and note that we can expect further significant developments in these areas in the years to come.

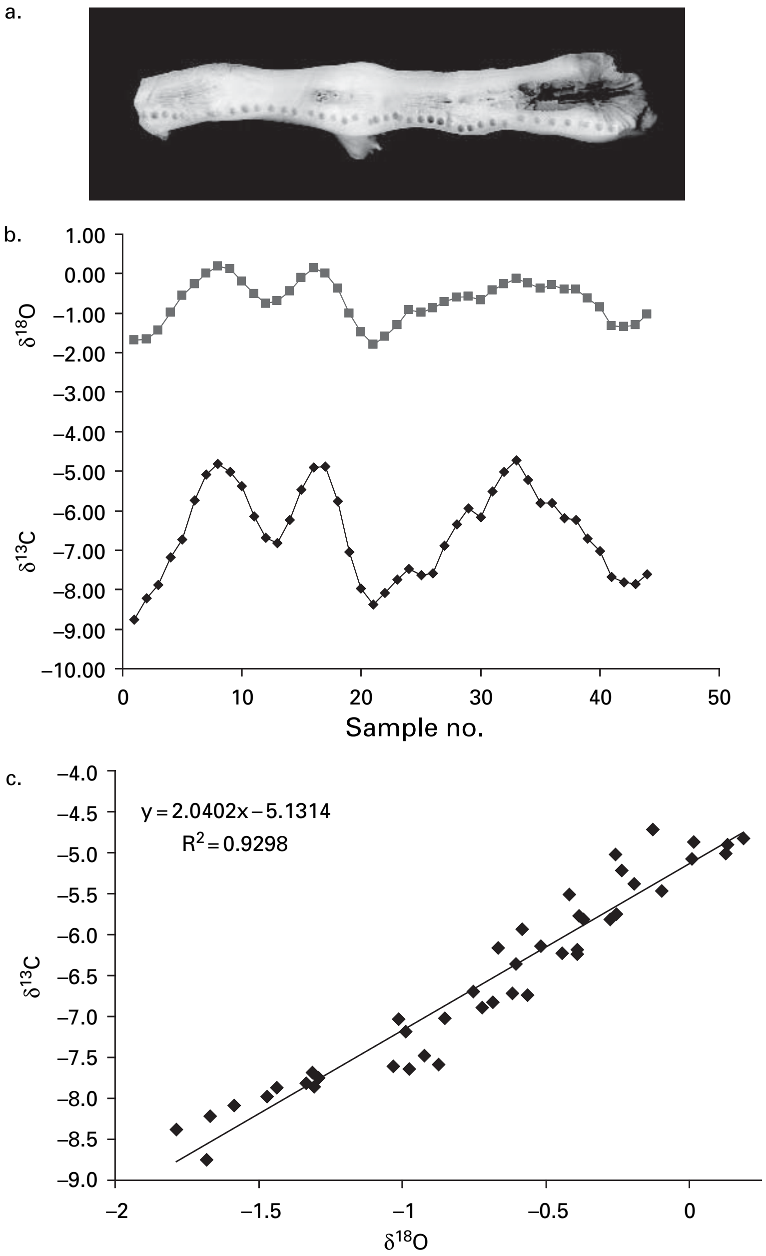


Fig. 7.5. (a) Longitudinal section of *Lophelia pertusa* drilled for carbon and oxygen isotope analysis. (b) Profiles of δ^{18}O and δ^{13}C along this section showing depleted signals at branch points (assumed to be annual). (c) Strong positive correlation between δ^{18}O and δ^{13}C. Note this relatively coarse sampling will have crossed growth lines present in the thecal wall. Figure reproduced from Spiro *et al*. (2000) with permission of John Wiley & Sons Ltd.

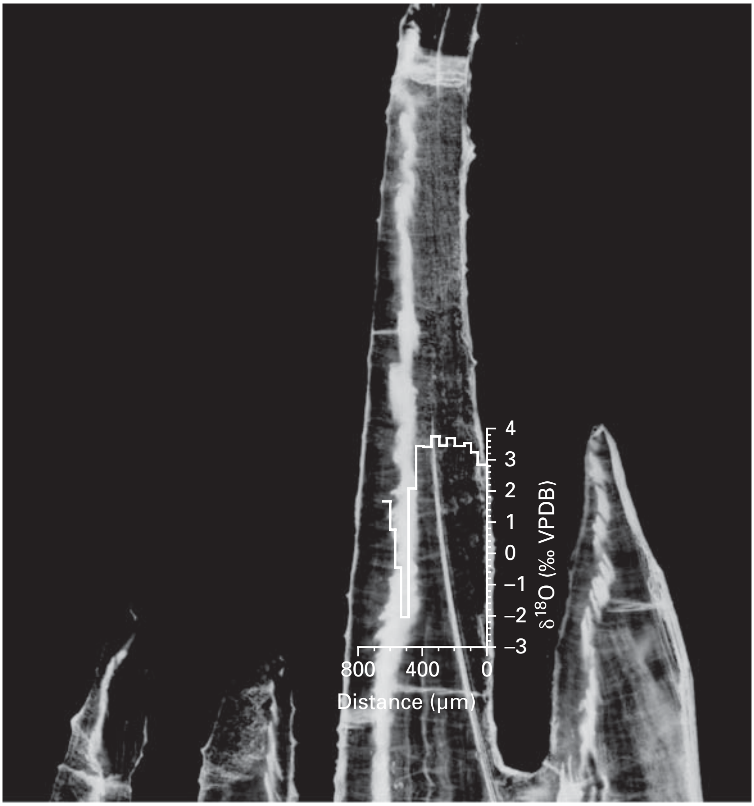


Fig. 7.6. A thin cross-section showing the white trabecular centre of calcification running the length of a septum from a *Desmophyllum dianthus* polyp. Microsampling the coral skeleton showed that this optically dense band is depleted in $\delta^{18}O$. Figure reproduced from Adkins *et al*. (2003) with permission of Elsevier.

There are currently two major hypotheses to explain vital effects in coral stable carbon and oxygen isotopes – the so-called ‘kinetic’ and ‘carbonate’ models. The kinetic model, outlined by McConnaughey (1989a, 1989b, 2003), explained vital effects as deriving primarily from kinetic fractionation of carbon and oxygen isotopes during calcification (with further deviations caused by ‘metabolic effects’ of coral respiration and, in the case of zooxanthellate species, symbiont photosynthesis). A kinetic isotopic effect is caused by the slightly different rates at which different isotopes react, with the stronger bonds associated with heavier isotopes making them marginally less reactive than lighter isotopes. In order for kinetic effects to become apparent they need to take place at a slow, rate-limiting stage before reverse reactions establish equilibrium. McConnaughey reviewed the steps in the calcification process and concluded that the only reaction slow enough to be susceptible to kinetic effects was the hydration and hydroxylation of CO_2 (see

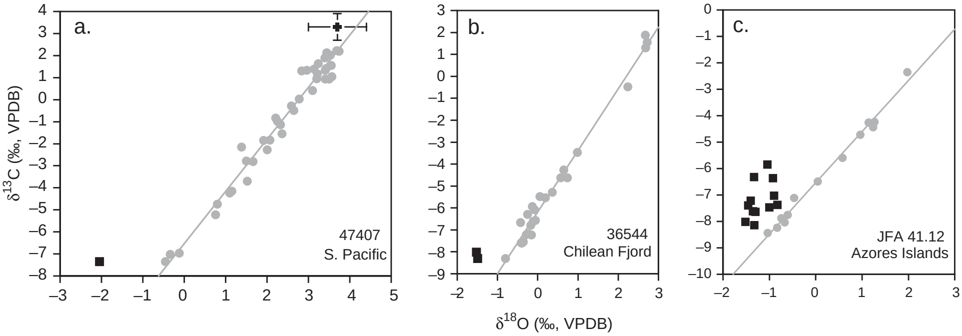


Fig. 7.7. δ^{18}O and δ^{13}C stable isotope plots from *Desmophyllum dianthus* showing the offset between values taken from trabecular centres of calcification (black squares) and other parts of the skeleton (grey circles). (a) Sample from the south Pacific (549 m) showing heaviest points at equilibrium (black cross) for δ^{18}O but slightly depleted for δ^{13}C. (b) Sample from a Chilean fjord (636 m). (c) Sample from the Azores (1000–2000 m). Figure reproduced from Adkins *et al.* (2003) with permission of Elsevier.

Equations 7.5 and 7.6 in Topic box 7.1). Thus if calcification quickly removes bicarbonate carbon produced by the hydration and hydroxylation of CO_2 any isotopic fractionation at this step will be preserved in the coral's skeleton. When calcification rates are low there is more time for CO_2 hydration and hydroxylation to approach equilibrium values of δ^{18}O and δ^{13}C. However, at more rapid calcification rates, bicarbonate is quickly removed and lighter δ^{18}O and δ^{13}C levels are recorded in the skeleton (since the CO_2 hydration and hydroxylation reactions discriminate in favour of light carbon and oxygen isotopes).

The second 'carbonate' model was proposed by Adkins *et al.* (2003) to explain trends in the relationship between ^{18}O and ^{13}C in cold-water coral skeletons, specifically those seen following high-resolution isotopic analysis of centres of calcification in *Desmophyllum cristagalli* (= *D. dianthus*) skeletons. Adkins *et al.* used a micro-mill to sample across centres of calcification and found that not only was there a strong relationship between band structure and stable isotope composition (Fig. 7.6), but that the values from the centres of calcification plotted off the main regression lines between δ^{18}O and δ^{13}C (Fig. 7.7). At the lightest isotopic values within the calcification centres, δ^{18}O continued to decrease but δ^{13}C values reached a plateau. Why should oxygen isotopes continue along the linear trend while carbon isotope fractionation does not? It was this key difference that led Adkins *et al.* to propose their model.

The carbonate model attempts to explain three consistent features of cold-water coral calcification: (1) the close correlation between δ^{18}O and δ^{13}C, (2) the breakdown of this relationship for δ^{13}C at the lightest values of δ^{18}O in the centres of calcification and (3) the gradient of the slope between $\delta^{18}O$ and $\delta^{13}C$. Adkins *et al*. proposed that, rather than the rate of calcification driving vital effect offsets, the pH of the extracellular calcifying fluid (ECF) was the ‘master variable’ determining vital effects. Following this reasoning, the coral is able to maintain the pH of the ECF using a cellular alkalinity pump (Ca-ATPase and/or proton ATPase) that removes two protons from the ECF for every Ca^{2+} ion transported. This creates a gradient between the lower pH of the cell and the higher pH of the ECF. High calcification and therefore high Ca^{2+} ion transport rates therefore equate with high ECF pH that in turn drive down the concentration of CO_2 (see Topic box 7.1). This means that as well as a pH gradient between the cell and ECF there is also a pCO_2 gradient promoting CO_2 diffusion into the ECF (recall that only uncharged CO_2 can cross cell membranes whereas charged ionic species cannot). Since CO_2 has a light isotopic signature, the coral skeleton would rapidly also acquire a light $\delta^{13}C$ value if the only carbon source was diffusing CO_2. In reality, however, the ECF is not a closed system and dissolved inorganic carbon (DIC) from seawater mixing with the diffusing CO_2 will determine the final $\delta^{13}C$ of the skeleton. Rapid calcification is produced by an active alkalinity pump creating a steep CO_2 gradient and a greater proportion of isotopically depleted CO_2-derived carbon appears in the skeleton – typified by the centres of calcification (light bands) in Fig. 7.6. In contrast, the dark bands in Fig. 7.6 correspond to slower calcification rates where a less active alkalinity pump allows more ambient seawater (heavier $\delta^{13}C$) mixing in the ECF. Importantly, there is a limiting maximum rate predicted by this model. When the pH of the ECF is so high that CO_2 is eliminated, the rate of CO_2 diffusion into the ECF reaches a maximum and cannot increase further. Therefore the proportion of isotopically lighter carbon from CO_2 versus heavier carbon from DIC cannot increase and the carbon isotope composition of the skeleton will stabilise, while oxygen isotopes may still fractionate further.

Adkins *et al*. also explain oxygen isotope vital effects as dependent upon this pH gradient but for different reasons. The $\delta^{18}O$ values of the separate components of DIC are greater than the $\delta^{18}O$ value of water, with carbonic acid having the most ^{18}O and the carbonate ion the least (thus more alkaline waters are relatively depleted in ^{18}O). Since the alkaline ECF promotes carbonate ion formation and this ion is isotopically lightest, the higher pH of the ECF also explains the lighter $\delta^{18}O$ of the skeleton. When the flux of CO_2 into the ECF reaches its maximum, the $\delta^{13}C$ of the skeleton is predicted to stabilise whereas the coral’s alkalinity pump can still increase the pH, creating a greater supply of isotopically lighter carbonate ions and a skeleton with a progressively lighter $\delta^{18}O$ (Fig. 7.8).

However, these models are by no means cut and dried explanations. Many issues remain. For example, only one study has tried to measure the pH of a coral’s ECF

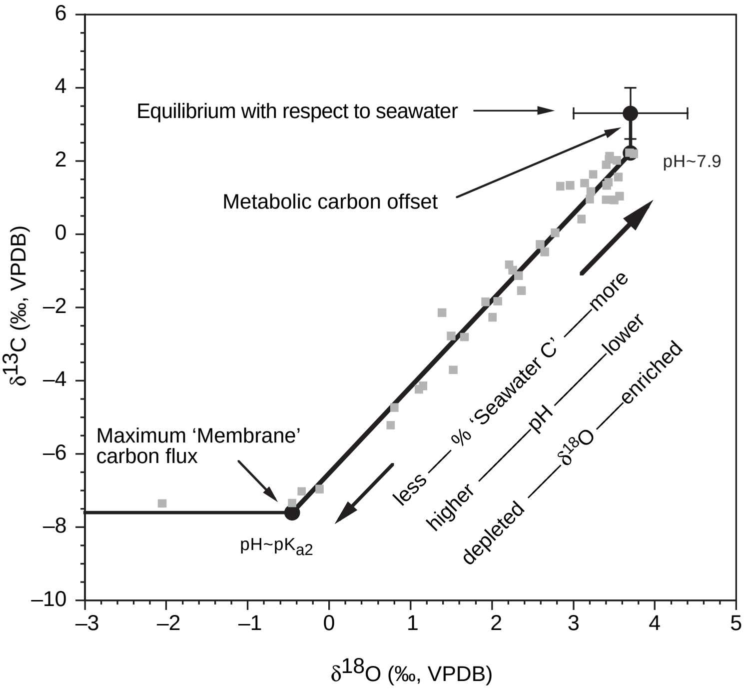


Fig. 7.8. Schematic graph summarising the concepts behind the carbonate model of Adkins *et al.* (2003). The coral skeleton is slightly depleted in δ^{13}C at δ^{18}O equilibrium by a small contribution of isotopically light respired CO_2. Dissolved inorganic carbon from surrounding seawater and CO_2 diffusing through the calicoblastic epithelium mix in the extracellular calcifying fluid. The pH gradient determines the rate of CO_2 diffusion and the value of δ^{18}O in the precipitating aragonite. When CO_2 diffusion reaches its maximum 'membrane' carbon flux the δ^{13}C of the aragonite cannot get any lighter but the δ^{18}O signature may still decrease since at higher pH oxygen from the predominant carbonate ions is relatively depleted in ^{18}O. Figure reproduced from Adkins *et al.* (2003) with permission of Elsevier.

(Al-Horani *et al.*, 2003) and the existence of such a space is hard or perhaps impossible to actually document histologically. Indeed it is perhaps better thought of as a virtual physiological 'compartment' rather than a physical space (Tambutté *et al.*, 2007a). Blamart *et al.* (2007) tackled some of these issues by seeing if boron isotope levels, a proxy for pH, supported the idea that portions of the coral skeleton, like the centres of calcification that show the greatest vital effects, were laid down from high pH fluids. Boron (^{11}B/^{10}B) is present in two forms in seawater: $B(OH)_3$ and $B(OH)_4^-$ with a distinctive 20‰ fractionation between these two aqueous species. The relative proportions of $B(OH)_3$ and $B(OH)_4^-$ depend upon pH. Crucially, only $B(OH)_4^-$ is incorporated into carbonate minerals so any boron isotopes in a coral's skeleton will reflect the amount of $B(OH)_4^-$ in seawater and provide a proxy for pH. Blamart *et al.* used an ion microprobe to examine δ^{11}B in centres of calcification and surrounding fibrous aragonite in *Lophelia pertusa* collected in the northeast Atlantic at 747 m depth. They found that δ^{11}B values in the centres of calcification were consistently lower than the surrounding fibrous aragonite, by up to 8‰. These data implied a pH of 8.9–9.3 in the centres of calcification and a *higher* pH of 9.4–10.2 in the surrounding fibrous aragonite. How can these findings be reconciled with the predictions of the carbonate model that the centres of calcification are deposited at higher pH (Adkins *et al.*, 2003)?

The answer is presently unknown. The findings of Blamart *et al.* (2007) are opposite to the predictions of the carbonate model and currently no geochemical model of coral calcification can account for the low δ^{11}B values in the centres of calcification. This implies that pH variations may not be the root cause of stable isotope vital effects in coral skeletons. The first attempt to measure pH underneath the calicoblastic layer was made by cutting a small hole at the base of a *Galaxea fascicularis* polyp and inserting a pH micro-electrode. In this zooxanthellate tropical coral, pH under the calicoblastic layer was higher than in the coelenteron or on the polyp's surface and was greater in the light, reaching a pH of 9.3, than the dark, where pH was about 8.1 (Al-Horani *et al.*, 2003). Recent work that has carefully examined the fine mineralisation pattern of coral skeletons and evidence that coral calcification is mediated by an organic matrix suggest that individual growth layers a few micrometres thick form individual 'environmental recording units' (Cuif & Dauphin, 2005a). There is clearly great need to consider appropriate analytical scales to avoid deriving geochemical signals from multiple recording units within the coral skeleton. With this in mind, the fields of coral geochemistry and biomineralisation seem poised so that in the years to come we can expect further interesting advances in our understanding of vital effects and the processes that control calcification.

Thus, vital effects are clearly a fundamental aspect of coral geochemistry evident not just in carbon and oxygen stable isotope composition but also in the patterns of trace element incorporation. For example, Sinclair *et al.* (2006) found that the rapidly calcifying centres of calcification in *Lophelia pertusa*, *Oculina varicosa* and *Desmophyllum cristagalli* (= *D. dianthus*) showed characteristic trace element signatures enriched in magnesium but depleted in uranium. High-resolution spatial sampling using ion microprobes and nano secondary ion mass spectrometry (NanoSIMS) has allowed the distribution of trace elements to be examined in greater detail (Meibom *et al.*, 2004, 2006, 2008). These studies show clearly that the trace element signature of centres of calcification differ markedly from surrounding fibrous aragonite. To explain these patterns, Meiboom *et al.* (2006, 2008) invoke a refined version of the 'organic matrix model'. This 'compartmentalised calicoblastic cell-layer' hypothesis rejects the presence of an

ECF in place of a thin film of a ‘hydro-gel’ skeletal precursor secreted by the calicoblastic ectoderm. Close cellular control differs in cells that are associated with producing centres of calcification from those producing fibrous aragonite, and so the calcification process is effectively compartmentalised with each compartment producing distinct skeletal elements with different trace element compositions.

In summary, whether mediated via kinetic, carbonate or other yet to be determined mechanisms, vital effects in isotopic and trace element composition relate strongly to the rate of coral calcification. In turn the rate of calcification in cold-water corals is ultimately controlled by the energy the animal expends on it. Cold-water coral growth rates (Section 3.4, p. 83) are largely controlled by their food supplies and reproductive periodicity (Section 3.6, p. 100) and, at high latitudes, seasonality in food supply may explain annual patterns in growth rate ultimately expressed through varying levels of vital effects in the coral skeleton. Thus the biology of the coral that determines the rate of calcification must underlie interpretation of the skeletal environmental proxies to which we now turn.

7.2 Temperature records

As we enter a time of rapid climate change, archives of past seawater temperature are a holy grail of palaeoceanography since records of previous ocean temperature and water-mass change are an essential component of our ability to predict future conditions. One of the first studies of a cold-water coral as a palaeoceanographic archive used a series of *Desmophyllum cristagalli* (= *D. dianthus*) fossils that spanned the Younger Dryas cool period (see Topic box 7.2). Smith *et al.* (1997) analysed carbon and oxygen stable isotope composition of *D. dianthus* from depths of 1600 m on Orphan Knoll in the northwest Atlantic. As described in the previous section, they also noted strong linear correlations between $\delta^{18}O$ and $\delta^{13}C$ but found that the slope of this relationship differed between corals growing in glacial and interglacial conditions. Dates from one specimen spanned the time period of the Younger Dryas, and the isotopic signature of about 3 mm of coral growth indicated this sudden cooling event may have begun over just five years.

Following up on these observations, Smith *et al.* (2000) examined this relationship in 18 azooxanthellate coral species collected from a variety of sites from Norway to Antarctica. All 35 specimens showed the same characteristic linear correlation between $\delta^{18}O$ and $\delta^{13}C$. Smith *et al.* used this linear relationship and known seawater temperatures for each specimen as the basis of the ‘lines technique’ to see if it was possible to produce a calibration that would reconstruct the

Topic box 7.2 **The Younger Dryas**

Earth's climate history has gone through periods of change from interglacial (or interstadial) warm periods, like the present day, to glacial (or stadial) cold periods when large polar ice caps and continental ice sheets dominated. These changes were driven by semi-periodic oscillations in the Earth's orbit that altered the input of solar energy. Other factors such as plate tectonics, changes in the Earth's atmospheric composition, variations in solar radiation, volcanism and meteorite impact are also implicated as agents of climate change. Climate shifts have been revealed in a variety of archives including, over the last 65 million years (Cenozoic era), $\delta^{18}O$ isotope analysis of Foraminifera from drilled sediment cores (Zachos *et al.*, 2001). The Younger Dryas cold period is an example of one particularly rapid climate change event that lasted 1300 years (~12 900 to ~11 500 years ago) following the Bølling–Alleröd interstadial at the end of the Pleistocene. It is perhaps the most studied climate change event of the last two million years although its causes have been contentious (Colman, 2007). Ice core records suggest that temperatures in Greenland cooled by 15°C in just a few decades at the start of the Younger Dryas. Cold-water coral evidence implies rapid cooling at one site in the North Atlantic happened in just over five years, a blink of an eye in palaeoceanographic terms (Smith *et al.*, 1997), see Section 7.2, p. 225.

What initiated this rapid cooling? The conventional explanation is that it was caused by a massive flood of glacial meltwater into the North Atlantic that disrupted thermohaline ocean circulation by freshening the northern Atlantic Ocean to the extent that surface waters were no longer dense enough to sink, so turning off North Atlantic Deep Water formation (Broecker, 2006). This flood is thought to have been caused by a diversion of water from the giant meltwater Lake Agassiz in the centre of the North American continent. Before the diversion, Lake Agassiz was believed to have drained south into the Gulf of Mexico, but as the Laurentide ice sheet retreated it seems that a new eastern drainage route opened through Lake Superior and the St. Lawrence lowlands, discharging a vast pulse of freshwater into the North Atlantic. This explanation is supported by several lines of evidence including geochemical proxy data from planktonic Foraminifera that show an increased freshwater input from the St. Lawrence River that could have reduced thermohaline circulation sufficiently to initiate the Younger Dryas cooling period (Carlson *et al.*, 2007).

But this may not be the whole story. Firestone *et al.* (2007) have put forward the intriguing idea that one or more large low-density extra-terrestrial objects exploded over North America 12 900 years ago, coincident with the start of the Younger Dryas cooling period. The single largest effect of these impacts would have been the destabilisation of the Laurentide ice sheet, which would have released icebergs and meltwater into the North Atlantic. As outlined by Broecker (2006) this massive release of freshwater would have weakened thermohaline circulation and sustained the cooling event for >1000 years. Firestone *et al.*'s evidence is based upon analysis of a carbon-rich black layer in the terrestrial record that also contains diagnostic indicators of an extra-terrestrial impact and associated biomass burning. Interestingly, the remains of Pleistocene megafauna including mammoths, mastodons and ground sloths are only found below this layer implying that this event also contributed to their extinction. However, this explanation may or may not be the whole story and we should expect more surprises as research continues into the Younger Dryas and other periods of rapid climate change.

temperature in which a coral grew from the δ^{18}O and δ^{13}C relationship alone (Fig. 7.9). Linear regression equations for these relationships take the form:

$$\delta^{18}\mathrm{O} = m\delta^{13}\mathrm{C} + b \qquad \text{(Eq. 7.8)}$$

where m is the slope and b the δ^{18}O intercept when $\delta^{13}\mathrm{C} = 0$. Smith *et al.* plotted the intercepts for each of their regression equations against temperature and found a strong negative correlation (Fig. 7.10). In turn, Smith *et al.* concluded that the linear regression equation from this relationship provided a tool to reconstruct seawater temperature estimates from δ^{18}O and δ^{13}C analyses of azooxanthellate corals with precisions estimated as ±0.5°C in cold waters (1°C)

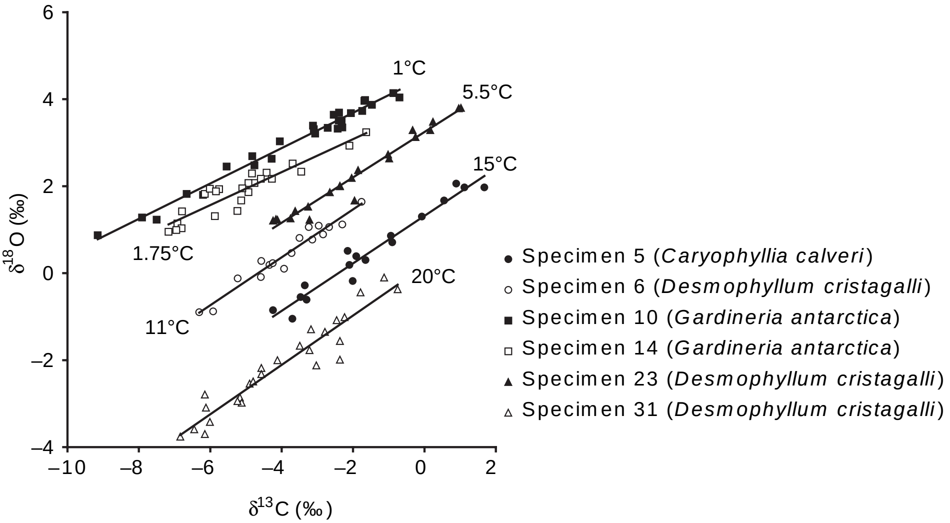


Fig. 7.9. The ‘lines technique’ of Smith *et al.* (2000) is based on the linear relationships between δ^{18}O and δ^{13}C in skeletal aragonite. Here data from six cold-water coral specimens from different temperature regimes are shown with regression lines for each dataset (*Desmophyllum cristagalli* = *D. dianthus*). Figure redrawn from Smith *et al.* (2000) with permission of the Society for Sedimentary Geology.

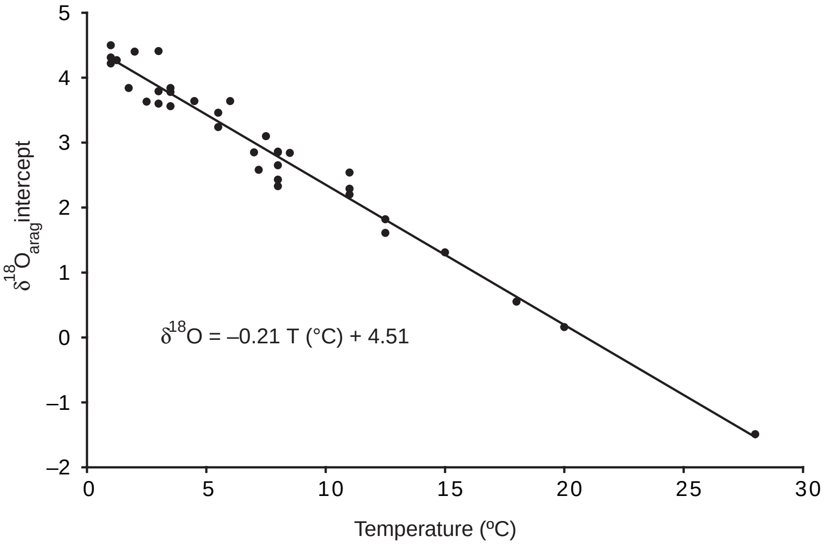


Fig. 7.10. The relationship between the $\delta^{18}O$ intercept when $\delta^{13}C_{arag} = 0$ for the 35 coral specimens analysed by Smith *et al.* (2000). Figure redrawn from Smith *et al.* (2000) with permission of the Society for Sedimentary Geology.

and ±2.1°C in warm waters (28°C). However, there are several issues with the lines technique including: (1) variability introduced by the coral's metabolic effects, (2) differences in slopes of the lines, (3) increasing uncertainty in seawater $\delta^{13}C$ values for pre-Holocene samples and (4) potentially confounding variability introduced if skeletal sampling crosses centres of calcification (Sherwood & Risk, 2007).

Early work attempting to use geochemical proxies to reconstruct temperatures from cold-water corals reported that coral growth rate-related kinetic effects masked any such environmental signals (Heikoop *et al.*, 2002). However, while some results remain quite preliminary, several studies are now showing that trace elements in cold-water corals have promise as palaeothermometers. Thresher *et al.* (2004) measured Mg/Ca ratios in two bamboo octocoral specimens (*Keratoisis* spp.) collected from 1000 m depth in the South Pacific. They found significant declines in Mg/Ca ratios across the growth zones of their specimens alongside increasing $\delta^{18}O$ values, which both indicated that the corals grew in gradually cooling seawater. Using Weinbauer *et al.*'s (2000) calibration of increased Mg/Ca by 0.005 (5 mmol mol^{-1}) per 1°C derived from *Corallium rubrum*, they estimated declines of 1.3 and 2.6°C in the two *Keratoisis* specimens. They interpreted this as evidence that deeper water masses shoaled by between 200–300 m, exposing the corals to decreasing ambient temperature and older ^{14}C reservoir ages (the latter supported by a mismatch between their

^{14}C ages and ages derived from other, independent approaches based on ^{210}Pb and U/Th dating and growth zone counts).

Magnesium/calcium ratios from the gorgonian octocoral *Primnoa resedaeformis* also show promise as palaeothermometers. Sherwood *et al.* (2005b) examined 17 northwest Atlantic specimens that had been growing since the 1950s at depths of 229–447 m off Atlantic Canada. They found a positive relationship between Mg/Ca in the calcitic portion of the corals' skeletons and temperature from instrumental records. In a parallel study, Sinclair *et al.* (2005) found significant noise in Mg/Ca profiles from *P. resedaeformis* analysed with both electron microprobe and laser ablation inductively coupled plasma mass spectrometry (ICP–MS) and recommended that several analytical profiles be used to develop temperature records.

Unlike Mg/Ca ratios, which increase with temperature, Sr/Ca ratios decrease with temperature. Initial evidence for a relationship between Sr/Ca and temperature was reported for specimens of cold-water corals belonging to the genera *Caryophyllia*, *Flabellum*, *Stephanocyathus* and one unknown specimen by Shirai *et al.* (2005), but once again, strong vital effects made these reconstructions difficult. Echoing the findings of Adkins *et al.* (2003), Shirai *et al.* noted that rapidly calcifying centres of calcification showed the most distinctive vital effects with higher Mg/Ca and lower Sr/Ca and U/Ca ratios than the surrounding skeleton and concluded that calcification rate was the most important factor determining micro-scale trace element distribution in the coral skeletons.

Cohen *et al.* (2006) report clearer temperature signals from both Mg/Ca and Sr/Ca ratios in *Lophelia pertusa* collected live from 129 m depth on the Tisler Reef, northeast Atlantic. They analysed skeletal material from two profiles, one along the vertical growth (linear extension) axis of the thecal wall and one across the outward (radial thickening) axis. The linear profile followed one translucent growth band next to the first centre of calcification, whereas the radial profile crossed successive crystal nucleation regions (centres of calcification). As found by Shirai *et al.*, Cohen *et al.* reported elevated Mg/Ca and depressed Sr/Ca ratios in the rapidly calcifying centres of calcification. Cohen *et al.* then correlated linear Sr/Ca profiles along the thecal wall to locally collected seawater temperature data, after filtering the data and assuming that maximum Sr/Ca ratios corresponded with minimum temperatures and vice versa. However, the amplitude of the Sr/Ca and Mg/Ca oscillations were too large to be explained by temperature effects on element partitioning alone. Cohen *et al.* concluded that seasonal changes in the saturation state of the coral's calcifying fluid (influencing skeletal 'precipitation efficiency'), along with a component of temperature-dependent trace element partitioning, could together account for the amplitude of trace element oscillations in *L. pertusa*. Thus, once again, the importance of understanding the coral's biology and, in particular, the likely seasonality of growth and food supply (Sections 3.3, p. 73 and 3.4, p. 83) are fundamental to understanding palaeoceanographic archives in cold-water corals.

It is also interesting to note that new temperature proxies are on the horizon. For example, Li/Ca ratios in both inorganic and biogenic carbonates, including the coral *Porites*, increase with decreasing temperatures making this a promising proxy for reconstructing past temperatures from cold environments, such as the deep sea (Marriott *et al.*, 2004). Indeed recent high-resolution laser ablation analysis of *Lophelia pertusa* samples collected from different temperature regimes suggests Li/Ca ratios in fibrous aragonite skeletal elements are primarily controlled by water temperature, making this an exciting proxy of intermediate water-mass temperature (Montagna *et al.*, 2008). Another promising temperature proxy, stable strontium isotopes ($\delta^{88/86}$Sr), has been examined in the shallow-water zooxanthellate coral *Pavona clavus* and shows clear temperature-dependent strontium isotope fractionation (Fietzke & Eisenhauer, 2006). Rüggeberg *et al.* (2008) analysed $\delta^{88/86}$Sr in *L. pertusa* samples taken from contrasting temperature regimes from southern (~10°C) to northern (~6°C) sites along the northeast Atlantic margin. They found a very similar temperature-dependent fractionation pattern suggesting that $\delta^{88/86}$Sr could also provide a useful intermediate water-mass temperature proxy from the remains of this ubiquitous cold-water coral.

7.3 Water-mass history

As noted earlier, the oceans are Earth's major heat transport system. Warmth from the tropics carried by the Gulf Stream and North Atlantic Drift currents gives northern Europe its comparatively balmy climate – palm trees grow on the west coast of Scotland, an unimaginable sight in Newfoundland (Canada) although it is closer to the equator. Thus wind-driven surface currents, like the Gulf Stream, transport heat from equatorial regions polewards where they cool, become more saline and sink (Fig. 7.11). This deep-water formation happens in the northern North Atlantic and Southern Oceans where surface waters are subjected to winter polar winds leading to evaporation and sea-ice formation as well as direct cooling. These processes combine to make surface waters colder and more saline to the extent that they eventually sink forming deep-water masses, the North Atlantic Deep Water and Antarctic Bottom Water, respectively. Given the importance of temperature and salinity in this process it is often referred to as 'thermohaline circulation'. Thermohaline circulation is also referred to as meridional overturning circulation and has been likened to a 'global conveyer belt' for the way it conveys heat from low to high latitudes.

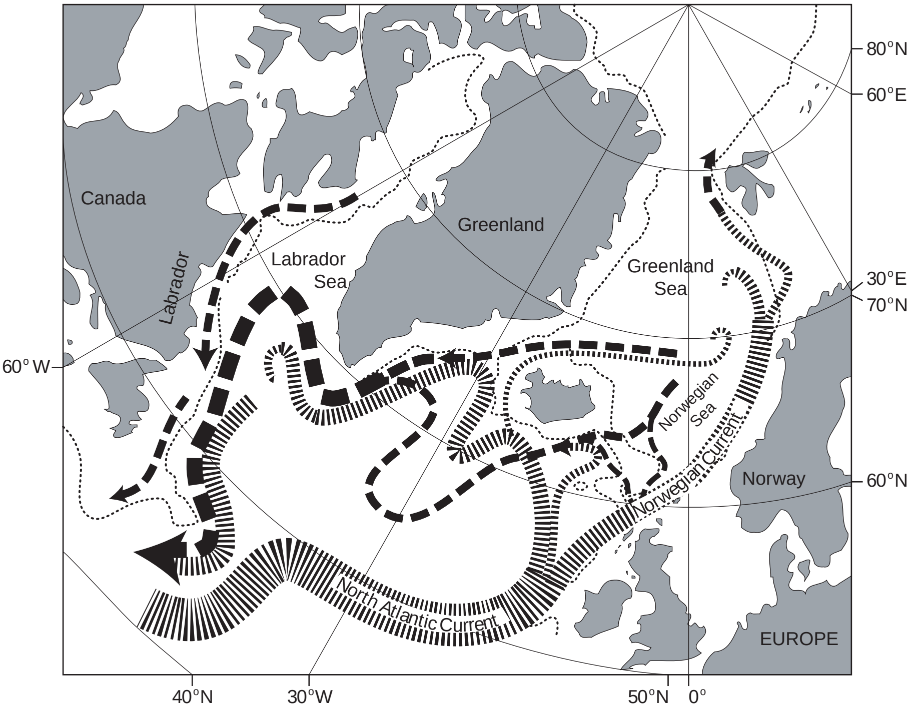


Fig. 7.11. As the Gulf Stream travels across the Atlantic becoming the North Atlantic Drift current it transports warm waters to northern Europe. The heat released from these surface waters is equivalent to a staggering 30% of the energy the North Atlantic receives from the sun (Broecker, 1987). As it cools in the Greenland Sea this water eventually sinks and returns south. This simplified diagram shows the major surface (narrow dashes) and deep (wide dashes) currents in the North Atlantic. Figure reproduced with permission from Stewart (2007), original figure courtesy of Woods Hole Oceanographic Institution.

Given its importance, tremendous efforts have gone into trying to understand the dynamics of thermohaline circulation. There is evidence that disruption to this circulation has caused rapid climate change, such as in the Younger Dryas (see Topic box 7.2), repeatedly in Earth's history (Broecker, 1997). Shifts in deep-water circulation patterns have been studied by following the history of water-mass mixing and aging. When dissolved inorganic carbon in seawater exchanges with carbon dioxide at the surface it will acquire a 'young' ^{14}C age corresponding to the atmosphere (radiocarbon is produced in the upper atmosphere), whereas deep-water masses that have not exchanged (or 'ventilated') with the atmosphere will have older ^{14}C ages. Therefore marine archives of dissolved inorganic carbon have the potential to reveal these so-called ventilation ages helping to understand the mixing and aging history of the oceans. However, as discussed in Section 3.4.2, p. 91, anthropogenic ^{14}C from atomic bomb testing will complicate this record as this spike in ^{14}C gradually mixes to deeper water masses. Radiocarbon ages for a water mass can be estimated if its ^{14}C content is known both when it forms and when it reaches the deep ocean. Ratios of $^{14}C/^{12}C$ are given as $\Delta^{14}C$, expressed as deviation from the $^{14}C/^{12}C$ ratio in a pre-industrial, pre-atomic era atmospheric standard (a nineteenth-century wooden tree ring-based record provides this standard).

As we saw in Section 3.4.2, p. 91, cold-water corals calcify using bicarbonate derived from dissolved inorganic carbon in seawater. Thus as they calcify they preserve a record of the ^{14}C from the seawater surrounding them. In the late 1990s two studies showed the value of cold-water corals in unravelling ocean ventilation history. The approach relies on parallel dating techniques, U/Th giving the coral's absolute age, and ^{14}C giving the age of the coral plus the age of the seawater DIC used in coral calcification (see Section 3.4.2, p. 91). By subtracting the U/Th age from the ^{14}C age it is possible to calculate the age of the water mass in which the coral grew. In the first study, Mangini *et al*. (1998) ran parallel U/Th and ^{14}C dating on a dead solitary coral (*Caryophyllia ambrosia*) recovered in a gravity core from 2306 m water depth in the Atlantic. The coral was estimated to have lived for approximately 200 years, 14 000 years ago. Mangini *et al*. found that the water mass in which the coral grew had a ventilation age of between 1077 and 1342 years, far longer than is the case today. In the second study, Adkins *et al*. (1998) also carried out U/Th and ^{14}C dating, this time on four *Desmophyllum cristagalli* (= *D. dianthus*) specimens from 1784–1954 m depth in the northwest Atlantic. Three of their *D. dianthus* showed a strange pattern of ^{14}C ages; they were younger in ^{14}C years at the base than at the biologically youngest growing edge of the polyp. This dramatically illustrated the effect of a change in water mass taking place around the corals. During their 160-year lifetimes these *D. dianthus* experienced shoaling of younger, low-nutrient North Atlantic Deep Water and its replacement with older, high-nutrient southern source water. This rapid change took place 15 400 years ago and implies a shoaling of southern source waters by at least 200 m during the transition to the Bølling–Alleröd warming period. Similar studies have subsequently used cold-water coral archives to examine ventilation histories in the Southern Ocean (Goldstein *et al*., 2001), North Atlantic (Schröder-Ritzrau *et al*., 2003; Frank *et al*., 2004; Cao *et al*., 2007) and, along with records from paired benthic-planktonic Foraminifera, radiocarbon ages from cold-water corals have been used to provide detailed glacial to Holocene histories (Robinson *et al*., 2005).

Recent work has used $\Delta^{14}C$ records from North Atlantic *Desmophyllum dianthus* that lived during the Younger Dryas to trace intermediate water-mass history during this well-studied recent period of rapid climate change. Eltgroth *et al.* (2006) collected seven *D. dianthus* from a series of North Atlantic seamounts at depths of 1069–2372 m. These corals were once again dated with parallel U/Th and ^{14}C dating approaches. Their absolute ages (11 330–12 700 years) spanned the Younger Dryas interval (see Topic box 7.2). From the Δ^{14}C they derived from *D. dianthus*, Eltgroth *et al*. concluded that these corals calcified from ^{14}C-depleted southern source water indicating that North Atlantic Deep Water either shoaled, or its formation was reduced and that a water mass akin to the present-day Antarctic Intermediate Water penetrated into the North Atlantic. These findings are fascinating given that disruption to thermohaline circulation is thought to have caused the Younger Dryas event.

Other approaches are emerging as potentially powerful means to trace water-mass history from cold-water coral archives. For example, van de Flierdt *et al.* (2006) used neodymium isotopes from *Desmophyllum dianthus* collected from the New England seamounts in the northwest Atlantic as a water-mass tracer. Neodymium ultimately derives from continental weathering and, like other rare earth elements, it is incorporated into a coral's aragonite skeleton approximately in proportion to its seawater concentration, free of vital effects. Since oceanic water masses have distinctive neodymium isotopic compositions these can be used as tracers to identify water mass. van de Flierdt *et al*. note that by combining ^{14}C, U/Th and neodymium isotope analysis of cold-water corals, one could derive a proxy of water-mass and ventilation history from the same absolutely dated archive – a valuable new resource for rapid climate change research.

7.4 Pollution and nutrient records

Recent work is also showing that cold-water corals may provide valuable archives of surface-water processes and even anthropogenic pollution history. Particularly promising results have been obtained from bamboo gorgonian octocorals and black antipatharian hexacorals whose skeletal banding structure is amenable to sclerochronology (see Section 3.4.1, p. 88). As well as providing time-referenced samples, the two-part calcium carbonate and organic components of some gorgonian skeletons provide an archive of dissolved inorganic carbon in the carbonate component and surface-particulate organic carbon derived from the coral's food in the organic component (see Section 3.4.2, p. 91). Evidence of amino acid stability over several thousand years (Goodfriend, 1997) shows that this organic material resists diagenetic change, making it also a valuable source of other isotopes such as nitrogen to assess trophic relationships.

The proteinaceous skeletons of antipatharian corals can be treated with weak potassium hydroxide to delaminate the skeletal bands so they can be carefully

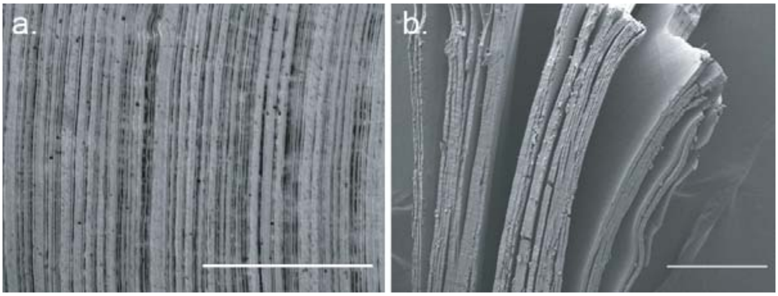


Fig. 7.12. (a) Cross-section under light microscope showing clear banding in the antipatharian coral *Leiopathes glaberrima*. (b) Scanning electron micrograph showing delamination after treatment for a week with potassium hydroxide. Scale bar 0.5 mm. Figures reproduced from Williams *et al*. (2006a) with permission of The Geological Society of America.

peeled apart and analysed separately, see Fig. 7.12 (Williams *et al*., 2006a). Using this approach, Williams *et al*. (2007) prepared bands from three *Leiopathes glaberrima* specimens collected between 307–697 m depth from the southeast USA and one specimen from the Gulf of Mexico (note taxonomic revision of this genus is ongoing, personal communication, D. Opresko, 2007). Using band counts and ^{210}Pb dating, these black corals' ages were estimated to be between 198–483 years. Williams *et al*. also analysed δ^{13}C and δ^{15}N compositions of the specimens and found evidence that the δ^{13}C signatures of the Atlantic specimens declined in concert with the greater release of isotopically-light anthropogenic CO_2 from fossil fuels (the Suess Effect). Nitrogen isotope values suggested that *L. glaberrima* feeds predominantly on nanoplankton at the base of the food chain. However, all four specimens showed a gradual δ^{15}N enrichment over their outer, most recently deposited bands, with the greatest increase seen in the Gulf of Mexico specimen. What could cause such a consistent change between specimens from different sampling areas? Williams *et al*. concluded that the most plausible explanation was that terrestrial manure and sewage pollution, which is enriched in δ^{15}N, enhanced nitrate δ^{15}N and this signal was transferred to the corals through the planktonic food chain. Interestingly, the Gulf of Mexico, where the strongest δ^{15}N enrichment was seen, receives more terrestrial manure and sewage-derived nitrogen than the waters of the coast off the southeast United States.

As well as recording surface events such as anthropogenic nutrient pollution, cold-water corals can provide a unique, long-term archive of nutrient status. Montagna *et al*. (2006) have shown that the ubiquitous workhorse of cold-water coral palaeoceanographers, *Desmophyllum dianthus*, can be used to reconstruct phosphorus concentrations. Their approach was to develop a calibration curve of skeletal P/Ca ratios from present-day *D. dianthus* against the dissolved inorganic

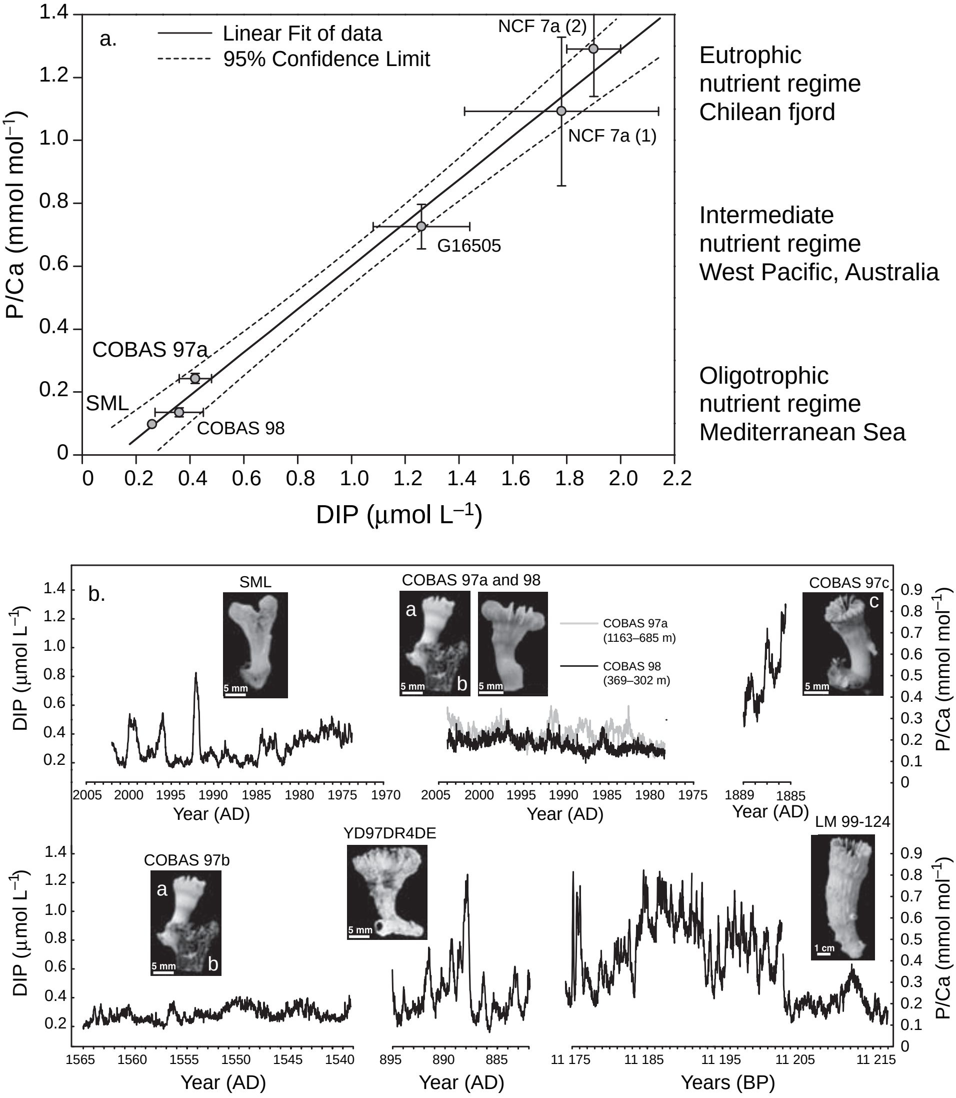


Fig. 7.13. Phosphorus levels in *Desmophyllum dianthus* can provide a proxy for seawater nutrient chemistry. (a) Linear regression of P/Ca ratios from *D. dianthus* specimens taken from contrasting nutrient regimes. (b) Reconstructed dissolved inorganic phosphorus (DIP) levels based on P/Ca analysis of a variety of *D. dianthus* specimens from the present day to the Younger Dryas. Sample COBAS 97a was dredged from deeper Mediterranean Sea waters with higher ambient phosphorus concentrations than sample COBAS 98 and this is reflected in the higher DIP levels in COBAS 97a. Note clear evidence for nutrient-enriched bottom waters at the end of the Younger Dryas (11 200 years ago, sample LM 99–124). Figure redrawn from Montagna *et al.* (2006) with permission of the American Association for the Advancement of Science.

phosphorus concentrations from the sites where the corals were growing. To span a range of phosphorus concentrations, Montagna *et al*. selected *D. dianthus* from contrasting nutrient regimes: (1) the primarily oligotrophic Mediterranean Sea, (2) the eutrophic northern Chilean fjords and (3) the Australian sector of the west Pacific (north northeast of Sydney), which has an intermediate nutrient regime between the Mediterranean and Chilean extremes. Fig. 7.13a shows the calibration produced from skeletal P/Ca ratios against the contrasting local dissolved inorganic phosphorus regimes experienced by the corals. This strong relationship allowed Montagna *et al*. to derive dissolved inorganic phosphorus concentrations from their P/Ca analysis of long-lived modern and long-dead, U/Th-dated specimens (Fig. 7.13b). The modern coral, from the western Mediterranean Sea, revealed increasing phosphorus concentrations over the last 30 years, reflecting the history of increased anthropogenic nutrient input to the Mediterranean over this period. The long-dead, sub-fossil coral results echoed findings from other studies and pointed to dramatic, rapid oceanographic and climatic change associated with the Younger Dryas. One of Montagna *et al*.'s specimens, dated to the end of the Younger Dryas, revealed evidence for dramatically elevated phosphorus levels, similar to conditions in present-day eutrophic Chilean fjords. This suggests that as humid conditions were established at the end of the Younger Dryas the increased intensity of the African monsoon and associated increases in terrestrial run-off from alpine glacial melting could have greatly increased phosphorus availability in the Mediterranean Sea. Interestingly, this proxy has also been applied to the shallow-water coral *Pavona gigantea* where P/Ca ratios accurately recorded known upwelling cycles in the Gulf of Panama (LaVigne *et al*., 2008).

This chapter can at best provide a quick overview of a complex and rapidly developing topic. While many issues remain to be addressed, and the problems of understanding vital effects in cold-water coral calcification cannot be underestimated, there is a large and growing body of work to show what a uniquely important archive of intermediate water-mass history cold-water corals can provide. However, while we are only now making progress in understanding the importance of this archive, it is becoming all too clear that many cold-water coral habitats have been damaged by bottom-trawl fishing and may be threatened by the spectre of ocean acidification. It is to the threats facing cold-water corals and our efforts to conserve them that we now turn.

8

Impacts and conservation

Know nature's children all divide her care;
The fur that warms a monarch warm'd a bear.
While Man exclaims, 'See all things for my use!'
'See man for mine!' replies a pamper'd goose:
And just as short of reason he must fall,
Who thinks all made for one, not one for all.
An Essay on Man
Alexander Pope (1734)

The ecosystems at the bottom of the deep sea are out of sight beneath the impenetrable grey of the waves. Any marine ecosystem, especially those of the deep sea, are remote from people's daily experience and may therefore be of little general interest. One of the greatest challenges facing deep-sea conservation is raising awareness of the hidden diversity and vulnerability of this, the largest and least-known environment on Earth. What is out of sight can all too often also be out of mind, but public perception of the threats facing some marine ecosystems, such as shallow-water tropical coral reefs, is relatively high – they are highly visual and popular holiday destinations for many people. But although out of sight and sometimes thousands of miles from the nearest land, cold-water corals and other deep-sea benthic ecosystems have been affected by human activity. Many, if not most, marine ecosystems have been affected by fishing and researchers regularly report deep-water trawl damage to cold-water coral and sponge habitats. Here we will describe present-day impacts, consider emerging threats and review what can and is being done to ensure their conservation.

8.1 Impacts

8.1.1 Fishing

Around the world, marine fisheries are declining. Studies in the last decade have highlighted the rapid loss of higher trophic level predatory species (Myers

& Worm, 2003), with progressively lower trophic level fish recorded in landings statistics since the 1950s. This trend has been termed 'fishing down the food web' from the economically most valuable predatory species to their less valuable prey (Pauly *et al*., 1998). Alongside mounting evidence that present-day fisheries are in crisis, we have realised that our ecological understanding of the marine environment, especially in shallow waters, is biased by the accumulated effects of generations of fishing activity (Jackson *et al*., 2001; Roberts, 2007). Therefore, we cannot rely on a sound baseline from which to measure and assess the changes wrought by fishing – this baseline has already been shifted and is continually shifting thanks to fishing activities around the world (Pauly, 1995).

Tragically, the depletion of fish stocks has been masked from public attention because as one stock is over-fished the fishing industry, often supported by government subsidies for both vessels and fuel (Pauly *et al*., 2002; Sumaila & Pauly, 2007), moves on to other areas and other fish populations. In his book *The Unnatural History of the Sea*, Roberts (2007) describes this history of serial depletion from the freshwater fisheries of Europe's rivers in the Middle Ages to the shallow seas and, with the advent of wind and notably steam-powered trawlers in the late nineteenth century, the continental shelf. As shelf fisheries collapsed in the mid-twentieth century the fishing industry has progressively fished deeper targeting long-lived, slow-growing deep-water species. This trend has brought fishing activity progressively into closer proximity with areas of the continental shelves, slopes, offshore banks and seamounts that support cold-water coral habitats.

From their earliest forays onto the continental shelf, fishers using gear that contacts the seabed have sometimes inadvertently fished corals, sponges and other benthic species. But it was the advent of bottom-trawl fishing where nets are dragged along the seabed that has caused most damage to cold-water coral habitats around the world. Trawling, or dragging as it is also known, is an extremely effective way of gathering bottom-living fish. Indeed, when longline and trap fishers brought their concerns that trawlers were damaging the seabed and disturbing spawning grounds to a UK Royal Commission in 1863, the Commissioners rejected pleas to control trawling in part because the trawlers were so successful in bringing fish to market (Roberts, 2007). Unfortunately trawling indiscriminately kills or damages non-target species caught in the mouth of the trawl, under the footrope and rollers, or under the large trawl doors that hold the net open. As trawling has expanded over time (Fig. 8.1) some areas of seabed have been trawled several times every year disrupting not just the benthic communities but the biogeochemical properties and integrity of seabed sediments (see review by Jennings & Kaiser, 1998).

For years coral and sponge-rich areas have been marked on fishing charts. In the northeast Atlantic, Faroese fishers refer to areas dominated by geodid and

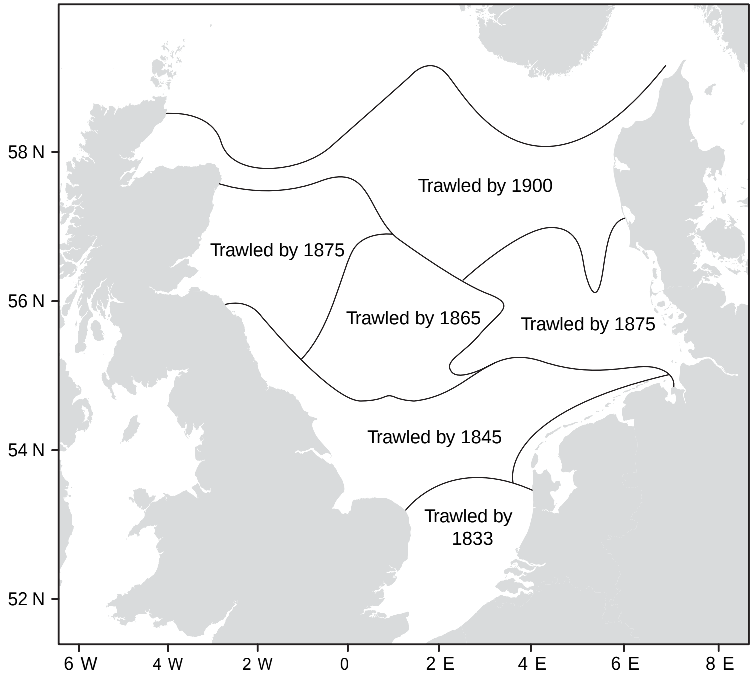


Fig. 8.1. The expansion of trawling in the North Sea pre-1900 by English fishers. Figure redrawn from Jennings and Kaiser (1998) with permission of the Academic Press.

other sponges as *ostur* or ‘cheese bottom’ because the smell, form and texture of the sponges reminded them of cheese (Klitgaard & Tendal, 2001). Trawl fishers have historically avoided such areas because they risked losing their nets in coral or spoiling the catch with sponge spicules. But as fishing vessels grew in size and trawl nets were strengthened with ‘rockhopper’ gear to ride across rough grounds, the risks to the gear decreased and the risks to benthic life increased. Scientific reports of trawling effects on cold-water corals were first made by Joubin in his 1922 paper *Les coraux de mer profonde* (The corals of the deep sea). Here he reported that the trawler *Tranche* sometimes brought up five or six tonnes of coral in a single haul – ironically his paper was subtitled *nuisibles aux chalutiers*, in other words the corals were a nuisance or damaging to the trawlers rather than vice versa.

However, the benthic impacts of deep-water bottom trawling only came onto the wider agenda in the 1990s as scientific interest in the ecosystem effects of fishing grew and the first pictures of the seabed scarred by trawling became available. Trawl marks at depths of 885 m to the north and west of Scotland were photographed as early as 1988 with subsequent surveys reporting trawl marks at

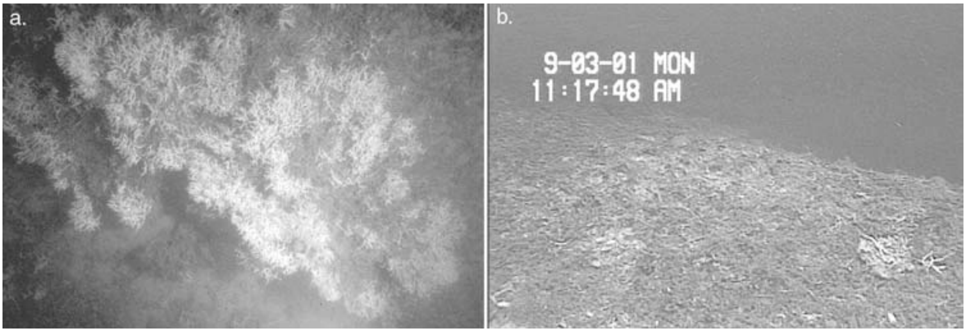


Fig. 8.2. Damage inflicted by bottom trawling to *Oculina varicosa* reef structure at 67 m depth off Florida. (a) Photograph taken in 1976. (b) Video frame grab from the same site reduced to rubble in 2001. Figure reproduced from Reed *et al.* (2007) with permission of the Rosentiel School of Marine and Atmospheric Science of the University of Miami.

depths over 1 km (Roberts *et al.*, 2000). Images of trawled and untrawled sites give the most stark and immediate picture of the effects of bottom trawling in cold-water coral habitats (Fig. 8.2, Colour plates 27, 28). As visual evidence that cold-water coral habitats had been degraded by bottom trawling accumulated, a scientific consensus was mounting that trawl fishing in vulnerable marine ecosystems dominated by epifaunal corals and sponges was unsustainable and should cease.

In 1998 Watling and Norse argued that disturbance by bottom trawling could be compared to terrestrial forest clearcutting since it converts a structurally complex, biodiverse habitat to one less diverse, flattened and homogenised. However, Watling and Norse noted two crucial factors that set trawling apart from clearcutting: firstly, trawling was largely unregulated and, secondly, it took place over an area 150 times larger than that clearcut annually. The same year, Norwegian government scientists went to sea to investigate reports from longline and gillnet fishers that cold-water coral reefs in their waters were being damaged by trawling and that this was reducing their catches. Fosså *et al.* (2002) subsequently described the results of ROV video surveys of these areas. In many instances they found that areas previously known to fishers for *Lophelia pertusa* reefs showed only scattered coral fragments or crushed and broken coral skeletons. The video surveys also showed lost trawl warps, nets and furrows ploughed through reef structures by the passage of heavy trawl doors along the seabed (Colour plate 28). Extrapolating from their findings, Fosså *et al.* speculated that between 30–50% of *L. pertusa* reefs in Norwegian waters had been damaged by trawling. These findings led to rapid legislation closing coral areas to all bottom fishing (Case study 8.1). Similar direct, unequivocal evidence for the physical damage of bottom trawling in cold-water coral habitats has now been reported in the waters of many other nations including Australia (Koslow *et al*., 2001), Canada (Gass & Willison, 2005; Mortensen *et al*., 2005), Ireland (Hall-Spencer *et al*., 2002; Grehan *et al*., 2005), New Zealand (Probert, 1997), the UK (Wheeler *et al*., 2005b) and the USA (Reed, 2002; Reed *et al*., 2007; Stone, 2006).

As well as visually obvious effects such as broken coral colonies or trawl marks scarring the seabed, bottom trawling disperses seabed sediments. Palanques *et al*. (2001) found that water-column turbidity increased three-fold for up to five days after experimental trawling in the northwest Mediterranean. The effects of sediment resuspension by bottom trawling on cold-water corals and sponges have not been examined in detail but such exposure could potentially smother or stress these suspension-feeding benthic animals. Although the wider ecosystem effects of deep-water bottom trawling have not been studied systematically there are some analogues. Cryer *et al*. (2002) collated information on the invertebrates caught in 66 continental slope bottom trawls by fishery scientists at 200–600 m depth north northeast of New Zealand. Although trawling began in this area before their study, Cryer *et al*. still found clear evidence that trawling reduced invertebrate species richness, diversity and density. After excluding the effects of depth and location, up to 40% of the variation in invertebrates caught could be explained by the level of trawling activity on this area of continental shelf.

Case study 8.1 **Conservation in national waters: Norway**

The first concerns over damage to Norwegian cold-water coral reefs of *Lophelia pertusa* were brought to the attention of government scientists by longline fishers in the mid-1990s. Subsequent video surveys in 1998 revealed areas of extensive damage and within a few weeks of this footage being broadcast on national television, the Norwegian Fisheries Minister was asked in Parliament how the government proposed to prevent such destruction. As a small, wealthy nation with sole control over its territorial seabed, Norway was well-placed to enact conservation measures quickly and the first area closed to any bottom-trawled gear was established just nine months later (a 978 km^2 area containing the Sula Ridge reef complex). Other factors reviewed by Armstrong and van den Hove (2008) also help explain how Norway was able to act so quickly: (1) since static fishing gear was not banned, protection was relatively uncontentious with longline and trap fishers, (2) government scientists were regarded as fair brokers, not party to either conservation or trawling interests and (3) a clear and open debate allowed members of the public and other stakeholders to participate. Since the closure of the Sula Ridge several other Norwegian areas have been closed to bottom fishing and any deliberate destruction of cold-water coral reefs is outlawed.

Case study 8.2 **Conservation in European waters: the Darwin Mounds**

The case of the Darwin Mounds closed area is interesting for several reasons. It is the first example of a cold-water coral conservation area in waters fished by several nations. It is also the first closed area made by the European Commission (EC) for nature conservation rather than fish stock management reasons. The Darwin Mounds were discovered during a wide-area environmental survey in 1998 by a group of UK oil companies, government regulators and academic researchers (Bett, 2001). The mounds, named after the research vessel *RRS Charles Darwin*, were initially identified on low-resolution side-scan sonar as features up to 75 m across and 5 m high that appeared to be related to local fluid escape processes. Cold-water corals (*Lophelia pertusa* and *Madrepora oculata*) preferentially colonised the mounds with fields of xenophyophores found in tail features extending downstream (Masson *et al.*, 2003). Subsequent high-resolution surveys suggest the mounds are in fact small coral banks trapping laterally transported sandy sediments (Wheeler *et al.*, 2008). Trawl marks crossing the mounds were identified in 2000 during these higher resolution surveys (Wheeler *et al.*, 2005b).

De Santo and Jones (2007) describe the interesting sequence of events that allowed the closure of the Darwin Mounds to happen. In 1999 the environmental group Greenpeace sued the UK government over its implementation of the European Union Habitats Directive, as part of its campaign to halt hydrocarbon exploration in the deep waters west of Britain (the 'Atlantic Frontier'). Greenpeace argued that the Habitats Directive should extend beyond 12 nautical miles to the full 200 mile territorial limit of the UK's exclusive fishing zone. In a landmark ruling in November 1999, the UK High Court accepted Greenpeace's case. Following this decision the UK began the process of designating the Darwin Mounds as a so-called 'Special Area of Conservation' under the Habitats Directive. After two years spent compiling information on potential offshore conservation areas, the UK made its first approach to the EC to close the Darwin Mounds in the autumn of 2002. Although this was received positively, there was no legal mechanism to close this area since it was fished by several EC member states under the European Union Common Fisheries Policy (CFP). However, the next step came the following year when reforms to the CFP gave the EC emergency powers to protect ecosystems from serious threats that required immediate action. After taking advice from the International Council for the Exploration of the Sea (ICES) and following informal discussions with other member states that fished this area (France and Spain), the UK again approached the EC to protect the Darwin Mounds in mid-2003. This resulted in two emergency closures followed by a permanent 1380 km^2 area closed to bottom fishing from March 2004 (see Fig. 8.8).

Experimental seabed dredging studies to simulate manganese nodule mining also provide a deep-water analogue of trawl disturbance. These studies have been carried out in the South Pacific ('DISCOL', Thiel *et al.*, 2001) and Indian Ocean ('INDEX', Sharma *et al.*, 2005). The DISCOL (disturbance and recolonisation) study began in the late 1980s to examine the effect of a simulated mining dredge disturbance at 4000 m depth in the Peru Basin, southeast Pacific (Thiel *et al.*, 2001). The DISCOL researchers used an 8 m wide plough–harrow device that was ploughed across the seabed where it penetrated the sediment by up to 15 cm. Disturbed and adjacent control sites were surveyed immediately after disturbance, and then again after six months, three years and finally seven years. Megabenthos were destroyed by the ploughing and replaced with motile scavengers. Sessile sponges, crinoids and gorgonian corals did not return within three years but after seven years these animals were recolonising. Compared to control areas distant from disturbance, the density of megafauna was reduced between ploughed tracks immediately after ploughing, implying that a sediment plume may have smothered these animals (Bluhm, 2001). Macrofaunal animals within ploughed sediments were also affected with their densities reduced to 40% of those in undisturbed areas and, although macrofaunal densities recovered within three years, the disturbed areas remained less diverse and were more heterogeneous after seven years (Borowski, 2001).

It seems likely that our baseline understanding of cold-water coral ecology has also been shifted by bottom trawling. In many parts of the world scientific surveys of cold-water coral habitats began in the late 1990s, often many years after the start of deep-water bottom trawling. Reports of coral bycatch by commercial fisheries are few and far between. Those that exist can be startling. Shester and Ayers (2005) collated US fishery observer data from the Aleutian Islands (see Case study 5.2, p. 150) between 1990 and 2002. During this time period over two million kilograms of coral and sponge bycatch were recorded, and during subsequent manned submersible dives to study Aleutian coral habitat, seabed disturbance from bottom fishing was seen on 88% of the transects corresponding to 40% of the total area surveyed (Stone, 2006).

8.1.2 Oil and gas

Mirroring the offshore trend of fisheries, the hydrocarbon industry is exploiting oil and gas reservoirs in progressively deeper waters. As shallower water hydrocarbon prospects such as the North Sea and northern Gulf of Mexico mature and become less profitable, technological innovations such as floating production platforms, riser systems and seabed-mounted pumping stations have allowed oil companies to move down the continental slope and drill in surprisingly deep waters. For example, in late 2003 the Toledo well was drilled at 3051 m water depth by Chevron Texaco in the Gulf of Mexico.

Hydrocarbon prospecting and extraction in the vicinity of cold-water coral habitats could have a range of potential impacts, although compared to the widespread abrasion of the continental shelf and margin by bottom trawling these effects seem likely to be more restricted in their extent. Of all the possible impacts the greatest seem to be the potential for drill cuttings to smother suspension-feeding corals and sponges. Cuttings are a mixture of the rock fragments produced during drilling and the fluids (drill muds), which often contain a suite of additives, used to transport the cuttings and lubricate and maintain pressure around the drill bit. When drill cuttings dispersal from an exploration well was examined in an area supporting *Lophelia pertusa* reefs (Træna Deep, ~300 m water depth, Norwegian shelf), cuttings were found to have dispersed up to four kilometres away and barite crystals from the drilling muds were found trapped within *L. pertusa* skeletal framework and polyp calices. However, it seems that because drilling discharges were relatively small scale from this particular exploration well and high current velocities rapidly dispersed cuttings, any negative effects on the coral reefs were limited, although the authors noted that more studies within 500 m of such drilling sites were needed (Lepland & Mortensen, 2008).

Many studies have examined the ecotoxicological effect of drilling fluid exposure on warm-water corals but, probably because of their inaccessibility and lack of standard aquarium maintenance protocols, there were no published studies of their effects on cold-water corals at the time of writing. Rogers (1999) reviewed the potential sensitivity of *Lophelia pertusa* and other cold-water corals to oil drilling and other activities. Studies that have exposed warm-water corals to drilling fluids have reported reduced viability (Raimondi *et al.*, 1997), morphological changes (Foster, 1980), altered feeding behaviour (Szmant-Froelich *et al.*, 1981), altered physiology (Krone & Biggs, 1980) or disrupted polyp behaviour (Thompson *et al.*, 1980). On balance, effects vary with species and a universal theme in these studies is that it proves hard to disentangle any toxicity effects from those induced by increased sediment load.

However, some cold-water corals have survived in close proximity to active drilling discharges. After an acrimonious debate on whether it should be dumped at sea, the North Sea oil storage buoy Brent Spar was towed to shore and decommissioned. As it was dismantled, large colonies of *Lophelia pertusa* were found to have colonised the base of the Spar (Bell & Smith, 1999). Subsequent ROV surveys showed this coral was widespread on northern North Sea oil platforms where it had developed a sexually reproducing, apparently self-seeding population (Roberts, 2002; Gass & Roberts, 2006), see Colour plates 12 and 13.

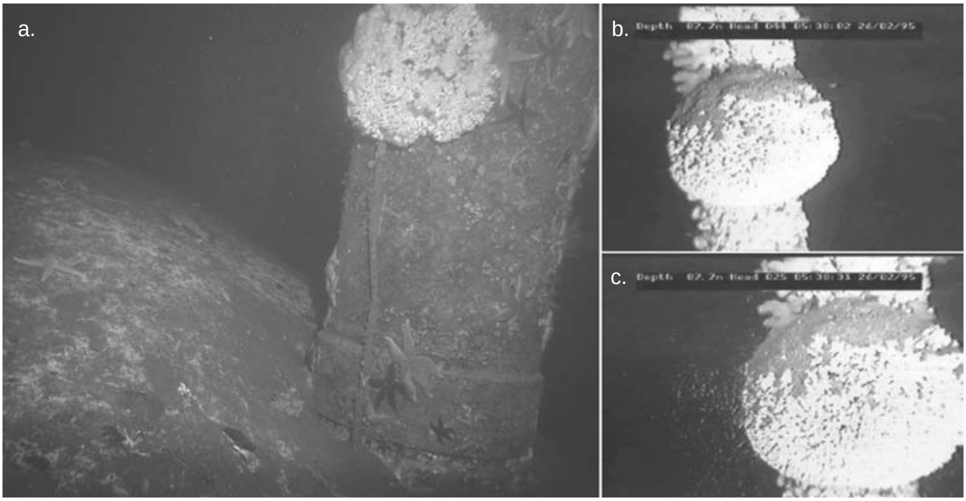


Fig. 8.3. *Lophelia pertusa* has colonised oil platforms in the North Sea sometimes growing close to drilling discharges. (a) Photograph of an *L. pertusa* colony attached to a platform leg just above a steeply sloping drill cuttings pile, itself colonised by white mats of *Beggiatoa*. (b) Video frame grab of an *L. pertusa* colony with a light dusting of unidentified sediment, possibly drill cuttings, subsequently resuspended by the ROV thrusters (c). Image (a), taken in 2002, is from the Heather platform, installed in 1977 at 144 m water depth, courtesy of Lundin Britain Ltd. Images (b) and (c), taken in 1995, are from the Brent Alpha platform, installed in 1976 (image from 88 m depth), courtesy of Shell UK Ltd.

Some of these coral colonies were found growing close to drilling discharge chutes or large drill cuttings piles on the seabed. In some cases drill cuttings had accumulated on a colony, smothering and killing the uppermost polyps while those on the lower half of the same colony were still alive (Fig. 8.3).

Despite this indirect evidence that *Lophelia pertusa* appears somewhat tolerant of drill cuttings discharge, it is important that controlled laboratory studies supported by *in situ* records of current regime and particle flux are completed to underpin our understanding of cold-water coral sensitivity to drilling discharges (Roberts, 2000). Scleractinian reef framework-forming corals, like *L. pertusa*, must tolerate ambient sediment exposure to some extent. Their occurrence in environments with actively mobile sediments, notably coral carbonate mounds (see Fig. 4.3, p. 112), indicates some capacity to tolerate or shed sediment particles. However this, and the occurrence of cold-water corals on oil platforms, cannot be taken as evidence that the reef habitats (corals and other fauna) are not vulnerable to stress from the additional sediment burden imposed by dispersing drill cuttings. More studies are needed to understand the fine balance between reef growth and the factors, like increased sediment stress, that might tip cold-water coral reefs from states of net growth to net (bio)erosion and reef degradation. This is especially true now, as progressive ocean warming and acidification (see below) are highly likely to raise baseline stress levels on these habitats in the years to come.

8.1.3 Mining

While sands and gravels have been dredged from shallow waters for many years, deep-sea mining is only recently becoming a commercial reality. Deep-sea manganese nodules were first discovered during the nineteenth-century *HMS Challenger* expedition but it took until the 1960s for the feasibility of mining them as a rich source of metals, notably cobalt, to be considered (Glover & Smith, 2003). The technical difficulties of recovering the nodules, combined with relatively low international metal market prices in the 1970s and 1980s, prevented commercial nodule mining. But improved undersea technology, driven in large part by the global oil industry's move to deeper waters, and exponential increases in metal prices since 2003, have brought deep-sea mining very much onto the agenda. At the time of writing two mining companies were actively pursuing deep-water mining interests to exploit so-called 'seafloor massive sulfide' deposits found with hydrothermal vents (Gill, 2007; Schrope, 2007). Nautilus Minerals, based in Canada, hopes to begin mining copper and gold in 1500 m water depth in the Bismarck Sea, north of Papua New Guinea in 2010 (Fig. 8.4). The London-based company Neptune Minerals has acquired rights to explore sulfide deposits in a 236 000 km^2 area extending through the Kermadec Arc, north of New Zealand, among other areas.

These initiatives have raised concerns that disturbance from mining operations, including sediment plumes and the release of toxic materials, could irreparably damage benthic ecosystems associated with the vents (Halfar & Fujita, 2007). The sites in the Kermadec Arc include a series of seamounts where epibenthic sledge sampling recovered over 300 macroinvertebrate species (6% previously unknown from New Zealand) and among these were 14 species of scleractinian and 7 species of antipatharian corals (Rowden *et al*., 2003). Since then, several species new to science have been described from the Kermadec Seamounts including the squat lobsters *Munidopsis kermadec* (Cubelio *et al*., 2007), *M. maunga* and *M. papanui* (Schnabel & Bruce, 2006), the decapod crustacean *Alvinocaris niwa* (Webber, 2004) and the deep-sea eelpout *Pyrolycus moelleri* (Anderson, 2006). As discussed in Section 5.3, p. 158, seamounts frequently function as ecological oases and may be significant centres of local endemism. Therefore any mining activities in such areas risk damaging or destroying biodiverse and potentially unique animal communities, with unknown implications in terms of lost biological resources.

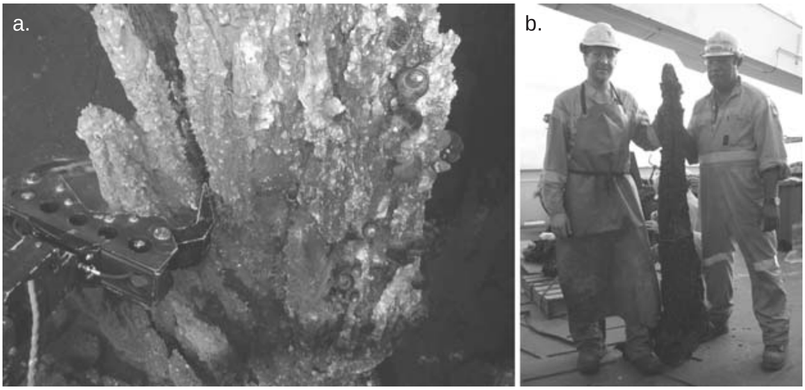


Fig. 8.4. Deep-sea mining is becoming a commercial reality. (a) A hydrothermal vent chimney being sampled by a deep-sea mining company. Several large gastropod molluscs (*Ifremeria nautilei*) can be seen on the right-hand side of the chimney (C. Van Dover, personal communication, 2008). For scale, the sampling claw is 40 cm across. (b) The deposits recovered, known as seafloor massive sulfides, are rich in copper and gold among other metals. Photographs courtesy of Nautilus Minerals Inc.

8.1.4 Climate change and ocean acidification

The effects of climate change on cold-water corals and the habitats they form are very poorly understood. Two components of climate change brought about by anthropogenic carbon dioxide release could directly affect cold-water corals: (1) increasing seawater temperatures caused by global warming and (2) progressive ocean acidification as this carbon dioxide dissolves in the oceans. Unlike the case of bottom trawling where a clear physical impact has been recorded, or the case of hydrocarbon extraction and mining where impacts from local extraction and sediment plumes can be understood at least in broad terms, the potential effects of climate change remain somewhat nebulous. However, if recent predictions are correct the effects of anthropogenic climate change, notably those of ocean acidification, could radically change the carbonate chemistry of the world's oceans with devastating implications for all calcareous organisms.

It is estimated that ~84% of global heating processes over the last 40 years have gone into warming the oceans (Levitus *et al*., 2005) and that although the signal is complex and varies by ocean basin, evidence to date shows this **ocean warming** has penetrated to depths of at least 700 m and is related to anthropogenic global warming (Barnett *et al*., 2005). As discussed in Section 2.3, p. 43, cold-water corals are typically restricted to relatively narrow temperature ranges and seem to respond dramatically to temperature changes. Elevated Mediterranean Sea temperatures in the summers of 1999 and 2003 caused mass mortality of the precious coral *Corallium rubrum* and subsequent study showed that deeper-dwelling colonies were more susceptible to elevated temperatures than shallow colonies (Torrents *et al*., 2008). When *Lophelia pertusa* was subjected to a 3°C temperature increase, within the range it experiences over a seasonal cycle, its metabolic rate increased three-fold (Dodds *et al*., 2007; see Section 3.5.1, p. 96). No studies have yet examined the consequences of such temperature sensitivity but at a simplistic level an animal whose metabolic rate triples will require an approximately equivalent increase in food input to compensate. It is unclear whether primary production in seawaters where the baseline temperatures have increased will necessarily compensate or whether any increase in production will flow through the food chain to higher trophic levels. What effect might these changes have on the local pelagic and benthic communities? Will important rates of benthic (bio)erosion also change, leading to increased or decreased erosion of cold-water coral colonies? Will temperature increases impose additional stresses on cold-water corals making them more susceptible to parasites and pathogens? The answers to these and other questions are unknown.

Anthropogenic carbon dioxide produced through fossil fuel burning, cement production, agriculture and deforestation has increased the concentration of atmospheric CO_2 from pre-industrial levels of about 280 ppm to about 385 ppm today with projections to over 1000 ppm by 2100 unless emissions are substantially reduced (Prentice *et al*., 2001). From Earth's historical perspective, atmospheric CO_2 concentrations have reached far higher elevations in the past, up to 7000 ppm in the Cambrian and 3000 ppm in the Cretaceous (Berner & Kothavala, 2001) resulting in greenhouse climates. The Palaeocene–Eocene transition (55 Ma) is marked by a global climate thermal maximum event associated with **ocean acidification** and the extinction of a large proportion of benthic calcifiers (Zachos, 2005). Significantly, the rate of change associated with the Palaeocene–Eocene transition event (several thousand years) is far slower than the present transition (decades to centuries) perhaps causing even greater ocean acidification in years to come (Turley *et al*., 2006). From a geological perspective, rapid shifts, such as the present-day changes, are considered extreme events that produced marked, long-term changes in the planet's functioning.

It has been estimated that the oceans have absorbed approximately 525 billion tons of carbon dioxide, roughly one-third of anthropogenic emissions (Sabine & Feely, 2007). This is now known to be affecting the carbonate chemistry of the seas with evidence from long-term near surface water monitoring showing progressively increasing pCO_2 and decreasing pH (Fig. 8.5). Modelling simulations have suggested that continued CO_2 release could cause ocean pH reductions of 0.7 units by 2100, potentially greater than anything except extreme events

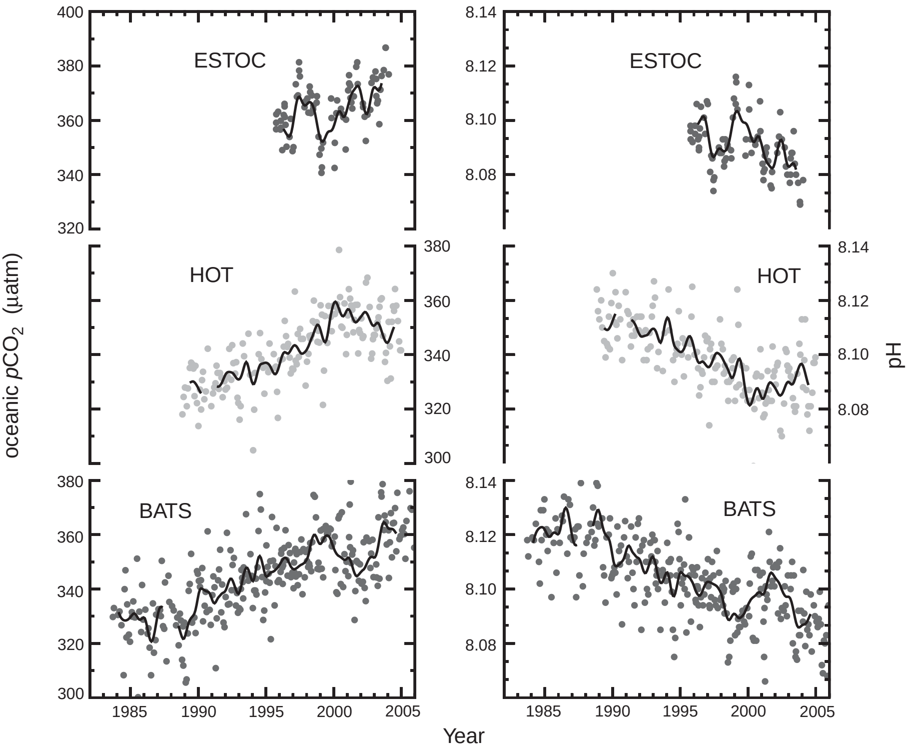


Fig. 8.5. Changes recorded in surface ocean *p*CO2 (left) and pH (right) from three time series stations: European Station for Time-series in the Ocean (ESTOC, 29°N, 15°W); Hawaii Ocean Time-series (HOT, 23°N, 158°W); Bermuda Atlantic Time-series Study (BATS, 31/32°N, 64°W). Values of pCO_2 and pH were calculated from DIC and alkalinity at HOT and BATS; pH was directly measured at ESTOC and pCO_2 was calculated from pH and alkalinity. The mean seasonal cycle was removed from all data. The thick black line is smoothed and does not contain variability of less than a six-month period. Figure reproduced from Fig. 5.9 (p. 404) in Bindoff *et al.* (2007) with permission of IPCC and Cambridge University Press.

experienced in the last 300 million years, and it is now generally agreed that surface ocean pH has already declined from 8.21 to 8.10 since the industrial revolution (Caldeira & Wickett, 2003; Feely *et al.*, 2008). A 0.1 unit drop may appear small; however, since pH is expressed on a logarithmic scale this apparently small decrease actually roughly represents a 30% increase in ‘acidity’, or the concentration of hydrogen ions.

As outlined in Topic box 7.1, p. 214, the carbonate chemistry of seawater depends on the interplay of equilibria between pH and the various chemical species of dissolved inorganic carbon present in seawater: dissolved carbon dioxide (CO_2(aq)), carbonic acid (H_2CO_3), bicarbonate (HCO_3^-) and carbonate

(CO_3^{2-}). As CO_2 dissolves in seawater it alters the equilibria between components of the carbonate system. Even though seawater is well buffered, the net effect of CO_2 dissolving is to increase acidity, lower pH and reduce the concentration of carbonate relative to bicarbonate (see Topic box 7.1, p. 214).

Orr *et al*. (2005) modelled the effects of carbon dioxide release on the carbonate saturation state of the world's oceans. Using the Intergovernmental Panel on Climate Change (IPCC) 'business as usual' scenario IS92a, where nations do little to limit emissions, the projections made by Orr *et al*. suggested that surface waters in the Southern Ocean will become undersaturated with respect to aragonite by 2050, with undersaturation extending throughout the Southern Ocean and into the sub-arctic Pacific by 2100. This effectively corresponds to a rapid shallowing of the aragonite saturation horizon. A spatial analysis by Guinotte *et al*. (2006) combined this shallowing with present-day occurrences of reef framework-forming cold-water corals (*Lophelia pertusa*, *Madrepora oculata*, *Goniocorella dumosa*, *Oculina varicosa*, *Enallopsammia profunda*, *Solenosmilia variabilis*). This showed that if Orr *et al*.'s predictions are correct then by the end of the twenty-first century about 70% of the present-day occurrences of these corals would be bathed in undersaturated seawater where net calcium carbonate dissolution would be expected (see Colour plate 29). These are stark projections, but what do they imply for cold-water coral habitats?

Without a firm grasp of cold-water coral calcification mechanisms or any understanding of how these species may respond to decreasing aragonite saturation states, we are entering a period of uncertainty just as our baseline knowledge of cold-water corals is starting to develop. It is possible that other ecosystem effects may come into play before direct effects of altered saturation state become apparent. As noted above, cold-water corals appear highly sensitive to temperature change. Any processes that affect food supply (see Section 3.3.3, p. 79) by altering primary production and/or local benthic–pelagic coupling could clearly impact all benthic organisms including cold-water corals, and ecological factors altering (bio)erosion levels could have far-reaching consequences for colony integrity. Studies of shallow-water tropical corals in laboratory aquaria and mesocosms have shown that scleractinian coral calcification is directly proportional to aragonite saturation (Gattuso *et al*., 1999; Marubini & Atkinson, 1999; Langdon *et al*., 2000, 2003; Leclercq *et al*., 2000; Marubini *et al*., 2001, 2003). On balance a doubling of atmospheric carbon dioxide causes anything from a 3–54% decrease in calcification (The Royal Society, 2005). As noted in Section 6.1, p. 175, gaps in the fossil record of scleractinian corals probably correspond to periods of altered ocean carbonate chemistry. The weight of present evidence suggests that the next age of ocean acidification has already begun and the prospects for cold-water corals appear bleak.

Fig. 8.6. *Corallium* jewellery displayed in a Sardinian shop window.

8.1.5 Coral collection

Some species of cold-water coral have been collected for hundreds or even thousands of years because their skeletons can be cut, shaped and polished to make jewellery (Fig. 8.6) or ground to powder and used in traditional medicines. The most heavily collected are species of the gorgonian *Corallium*, frequently known as red, pink or precious coral (see Section 2.2.4, p. 37), but *Allopora californica* (a hydrocoral) along with antipatharian (black), isidid (bamboo) and *Gerardia* (gold) corals are also collected for jewellery. Traditionally, precious corals were collected by free diving or by tangle-net dredges, such as the *ingegno* or St. Andrew's Cross that was used in the Mediterranean Sea until 1994 when it was banned by the European Union. These tangle-net dredges work by breaking the corals from the seabed (along with any other epifauna) and so, like bottom trawls, operate indiscriminately and are very damaging to benthic life. Shallower species have been collected by Scuba diving and in Hawaii deeper-dwelling *Gerardia*, *Corallium* and antipatharian corals have been collected by manned submersibles (Grigg, 1993, 2002). The Hawaiian authorities used a fishery management plan developed in the 1970s to estimate maximum sustainable yields for coral collecting (Grigg, 1976). However, more recent work on the growth and age of the collected corals shows that earlier assumptions of annual banding patterns were flawed and that species like *Corallium secundum* were very much older and slower growing than initially estimated (Roark *et al.*, 2006; see Section 3.4.2, p. 92).

Following the pattern of many deep-water fisheries, precious coral collecting has boomed following the discovery of a commercially viable area and then collapsed as the coral population becomes depleted (Fig. 8.7). For example, in 1965 Japanese coral fishers discovered beds of *Corallium secundum* at 400 m

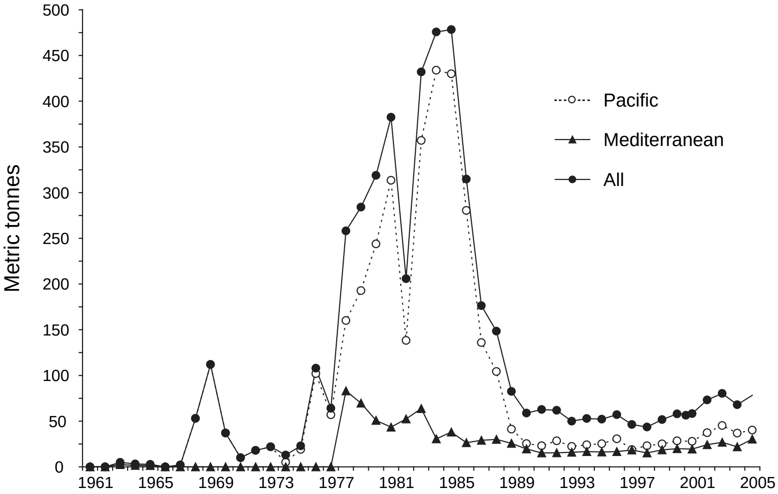


Fig. 8.7. Graph showing global collection of *Corallium* species recorded by the UN Food and Agriculture Organisation between 1961 and 2005. Species from the Pacific (Asia) are *C. elatius*, *C. japonicum*, *C. konojoi*, *C. rubrum*, *C. secundum* and a currently undescribed species. Species from the Mediterranean (Europe and Africa) is *C. rubrum*. Figure courtesy of E. Neeley.

depth on the Milwaukee Banks in the Emperor Seamount Chain. Coral collection peaked four years later at 150 tonnes per year then collapsed until new, deeper coral populations were found at 900–1500 m depth. At its peak in 1981 this new coral fishery collected 200 tonnes from the Emperor Seamounts after which yields declined and the fishery was abandoned in 1989 (Grigg, 1993). There is now a general consensus that precious coral collection is unsustainable.

As well as the benthic impact of tangle-net dredges, recent studies have shown that precious coral collection has had negative consequences for exploited populations. Tsounis *et al*. (2006) compared Mediterranean *Corallium rubrum* populations from fished areas with those in a marine reserve and found that the corals in the reserve were both older and larger than those in fished areas. This is significant both in terms of habitat provision and also because larger gorgonians may be the most reproductively active. But as well as impacting on population size structures, *Corallium* collection also seems to have affected population genetic structure. Baco and Shank (2005) found evidence that *C. lauuense* populations from fished areas of the Hawaiian Islands could be suffering from inbreeding depression due to a local population bottleneck brought about by coral collection during the 1970s.

Ironically, despite the growing evidence that *Corallium* collection is unsustainable and although this species is extensively collected and traded, it is not listed by the Convention on International Trade in Endangered Species (CITES).

On the other hand, all scleractinian, antipatharian and stylasterid corals are listed, whether or not there is any evidence that they are endangered. These groups are all listed in Appendix II corresponding to ‘species not necessarily now threatened with extinction but that may become so unless trade is closely controlled’. In 2007, the USA put forward a proposal to add all *Corallium* species to CITES Appendix II. The proposal was initially accepted only to be later rejected by secret ballot with further discussion blocked by those nations that actively export *Corallium* (E. Neeley, personal communication, 2008).

8.1.6 Other threats

Other human activities could degrade cold-water coral habitats if appropriate environmental assessments are not carried out. Submarine telecommunication and electricity cables along with oil and gas pipelines can all be laid across vast distances and at great depths. Cables are frequently buried in shallow trenches to help protect them from, among other things, trawling damage. With adequate mapping and careful placement, cable and pipeline laying and any associated vessel anchoring should be a well-managed and relatively low impact activity. For example, the route of the Haltenpipe gas pipeline in mid-Norway was chosen to avoid *Lophelia pertusa* reefs (Hovland *et al*., 1994b). In addition to the fishing, hydrocarbon-drilling, mining and climate-change effects discussed above, Glover and Smith (2003) reviewed a suite of human impacts on deep-sea ecosystems including waste disposal. Sources of waste could include shipwrecks, oil platforms, munitions, radioactive materials, sewage sludge, dredge spoil and carbon dioxide sequestering programmes.

Carbon dioxide sequestration into geological formations such as depleted oil and gas fields has been proposed as a way of reducing atmospheric CO_2 release. Since 1996 the Norwegian state oil company Statoil has been stripping CO_2 from natural gas produced at the Sleipner field in the northern North Sea and has re-injected roughly eight million tonnes of CO_2 into a 200 m thick saline aquifer. The CO_2 in these strata has subsequently been tracked and modelled using seismic reflection profile data (Bickle *et al*., 2007). Clearly any accidental release of CO_2 near cold-water coral habitats could have significant implications for local carbonate chemistry and the integrity of corals and other calcareous organisms. Pumping liquefied CO_2 directly into the deep sea has also been put forward as a disposal method. At the time of writing, only small-scale experiments releasing liquid CO_2 at depths of up to 3627 m in the Monterey Canyon, northwest Pacific had been carried out. In these disposal experiments Brewer *et al*. (1999) found that liquid CO_2 quickly reacted with water forming a CO_2 hydrate ($CO_2 \cdot 6H_2O$), in an exothermic reaction that would generate heat alongside the hydrate. It is generally agreed that any deep-sea organisms coming into contact with large-scale CO_2 disposal would be killed (Davies *et al.*, 2007) and over time the hydrate would slowly dissolve spreading CO_2 through the deep ocean (Broecker & Kunzig, 2008, p. 214), disrupting carbonate chemistry and making the seawater more acidic. The wider implications of CO_2 disposal on neighbouring deep-water habitats are not understood, but clearly any phenomena creating local ocean acidification will impact upon all calcareous organisms.

As with other human activities, research science survey and sampling operations can affect cold-water coral habitats, though the scale of scientific sampling is vastly less than other human activities. However, research scientists and their funding agencies should be duty bound to ensure that scientific sampling is minimally invasive and any intensive sampling of small geographical areas should be carefully considered and monitored. Any future bio-prospecting operations for novel biomedical compounds must be carefully controlled and carried out in similar ways to avoid local ecosystem damage. The traditional dredge and trawl sampling techniques of the eighteenth, nineteenth and early twentieth centuries are now largely surpassed with targeted samplers deployed from manned submersibles, ROVs or video-directed cores and grabs (see Section 1.2.3, p. 15). Naturally, as well as avoiding collateral damage, such sampling provides all-important precise information on a sample's location and depth along with valuable extra context in terms of the local seabed and habitat type, not to mention a suite of environmental data routinely collected by research submersibles (e.g. temperature, salinity, oxygen, etc.).

8.2 Conservation

Any conservation activity, be it terrestrial or marine, for a single species or an ecosystem, is an activity undertaken to change destructive human behaviour and use of the environment. As we have seen, cold-water corals are threatened at the species, habitat and wider ecosystem levels. For example, at the species level *Corallium* and other precious corals have been depleted by commercial collection for jewellery. At the habitat level deep-water bottom trawling has caused widespread damage and the emerging threats of climate change from ocean warming and acidification may fundamentally perturb all marine ecosystems. Conservation measures are conceptually simple – damaging activities can be outlawed in networks of marine reserves and anthropogenic carbon dioxide emissions can be curtailed. But the reality of bringing about such changes in human behaviour is enormously complex. Without enforcement, marine reserves (known as 'paper parks') are almost worthless. The first marine protected area to conserve cold-water coral reefs was established in 1984 to protect *Oculina varicosa* habitat off the coast of Florida, but by 2001 even the reefs within this area, and many of those outside, had been reduced to rubble by shrimp trawlers (Reed *et al*., 2007). It is probably no exaggeration to say that curtailing anthropogenic CO_2 emissions and adapting our society from its reliance on fossil fuels is the greatest environmental challenge humanity has faced.

8.2.1 Protected areas

Marine reserves (also referred to as marine protected areas, marine sanctuaries, no-take zones, etc.) are defined by Norse *et al*. (2005) as places that are permanently protected from all preventable anthropogenic threats. The qualifier *preventable* allows that some anthropogenic threats, such as pollution or the effects of climate change, will transcend reserve boundaries. Research since the 1990s is now building a picture of the effects of marine reserves in shallow-water environments. Halpern (2003) reviewed 89 studies of marine reserves and found on average that density, biomass, organism size and diversity were all greater in reserves, or after they were established, than they were outside or before the reserve came into effect. At the time of writing no similar studies of deep-water marine reserves were available and since these have only been established recently and many deep-water species are long-lived and slow-growing it may take many years for any reserve effects to become apparent.

Following the creation of the *Oculina varicosa* ‘habitat area of particular concern’ in 1984, conservation areas for cold-water corals have been established in several parts of the world. Most, if not all, of these have been created to control damage by bottom trawling and most have been created since the late 1990s. Many are not true marine reserves since, although anthropogenic activities such as trawling are outlawed, other activities such as longline or trap fishing are frequently still allowed. In a report for the United Nations Environment Programme’s World Conservation Monitoring Centre, Freiwald *et al*. (2004) collated information then available on cold-water coral protected areas. This report described measures, including established protected areas, to help conserve cold-water corals by the governments of Australia, Canada, New Zealand, Norway, the UK, the USA and internationally by the European Commission (see Table 1 in Davies *et al*. (2007) for an updated list). The speed with which these measures have come into effect varies tremendously reflecting the time it takes to achieve consensus, especially in an international context (see Case studies 8.1 and 8.2).

Cold-water coral conservation efforts are currently restricted to wealthy, developed nations. Refinements and extended use of the predictive habitat suitability modelling approaches described in Section 5.6, p. 168 offer the opportunity to identify areas of habitat suitable for cold-water corals in other regions of the world. Interestingly, this approach may help implement the recent United Nations

Case study 8.3 **The United Nations and vulnerable marine ecosystems**

In 2002 the UN Informal Consultative Process on Oceans and Law of the Sea (UNICPOLOS) recommended that the United Nations General Assembly improve the management of vulnerable deep-sea ecosystems. In 2003 and 2004 petitions were gathered at scientific conferences and a consortium of non-governmental organisations formed a Deep-sea Conservation Coalition to lobby the UN to impose a moratorium on high seas bottom trawling. This culminated in late 2006 with UN General Assembly resolution 61/105, paragraph 80, subsection 10 ‘Responsible fisheries in the marine ecosystem’:

> Calls upon States to take action immediately, individually and through regional fisheries management organizations and arrangements, and consistent with the precautionary approach and ecosystem approaches, to sustainably manage fish stocks and protect vulnerable marine ecosystems, including seamounts, hydrothermal vents and cold water corals, from destructive fishing practices, recognizing the immense importance and value of deep sea ecosystems and the biodiversity they contain.
>
> (UN, 2007).

While this stopped short of an outright moratorium this represents a crucial statement of the precautionary principle in developing international policy for high seas conservation and the future protection of vulnerable marine ecosystems including cold-water corals.

declaration that individual nations and fishery management organisations protect vulnerable marine ecosystems, including cold-water corals, from destructive fishing practices where they are known or are *likely* to occur (Case study 8.3). There is a great need to extend this approach and support the basic seabed mapping and habitat characterisation needed to describe deep-water ecosystems in the waters of developing nations. Only with progress in these areas can we hope to achieve ambitious targets such as those set at the 2002 Johannesburg World Summit on Sustainable Development. Although without funding to achieve their goals, these targets included a series of marine reserve networks consistent with international law and scientific information to be established by 2012.

8.2.2 Monitoring

As noted earlier, protected areas are only effective if they are monitored and enforced. In the marine environment, and especially far from shore above the continental shelf, margins and offshore seamounts where cold-water corals frequently occur, monitoring is challenging because any protected areas will be remote, inaccessible and therefore expensive to police. Historically many nations have maintained fishery protection fleets, surveillance aircraft and individual observers on board fishing vessels to monitor offshore fishing activities in their waters. However, since the late 1990s new approaches to vessel monitoring have begun to be used. These rely on two remote sensing techniques: (1) a vessel monitoring system that records fishing vessel positions via satellite, which requires the fisher's compliance, and (2) detecting vessels using visual or radar satellite surveillance techniques that are independent of the fisher and so provide a valuable check on the vessel monitoring approach.

The vessel monitoring system (VMS) broadcasts its global positioning system (GPS) position from a unit mounted on the vessel at a pre-determined interval. The system can also transmit other data including vessel speed, useful in deducing whether a vessel is steaming or trawling. In recent years, VMS units have become more widespread. For example, since 2000 European Union vessels >24 m length have been required to transmit VMS positions at least every two hours, with this requirement extended in 2005 to all vessels >15 m length. Mills *et al.* (2007) examined VMS data collected from UK beam trawlers in the North Sea between 2000–3. They found that even though data points were often only available every two hours it was still possible to identify trawling from steaming in much the same way as biologists can discriminate between feeding and foraging behaviours using animal tracking data. Davies *et al.* (2007) also used VMS data filtered to retain vessel speeds compatible with trawling to examine trawling

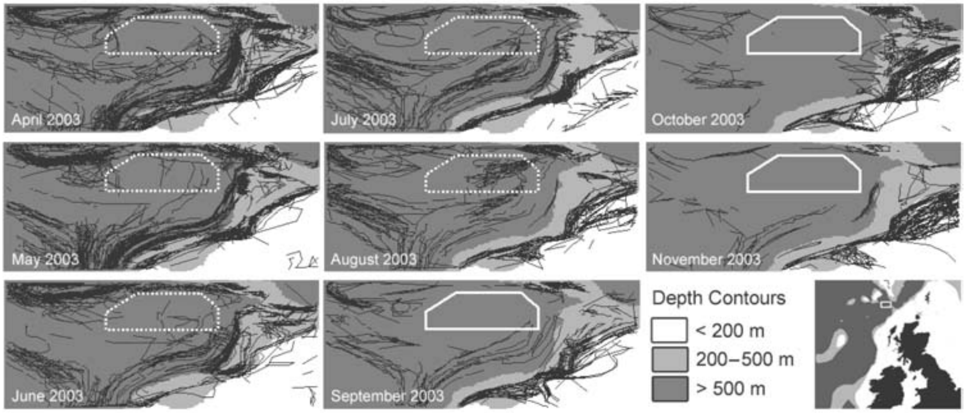


Fig. 8.8. Vessel monitoring system tracks of fishing boats travelling at typical trawling speeds (1.5–4.5 knots) in the vicinity of the Darwin Mounds closed area. The closure came into force in September 2003. Small inset map shows the location of the Darwin Mounds in the north Rockall Trough (white box). The VMS tracks appear to indicate an increase in trawling in the designated closed area the month before closure (August 2003), but this may reflect a seasonal increase in trawling activity. Figure reproduced from Davies *et al.* (2007) with permission of Elsevier.

patterns around the Darwin Mounds closed area (Fig. 8.8). They found that, as expected, trawling patterns followed the contours of the shelf edge and offshore banks and that immediately after the closure came into force, trawling within the closed area was noticeably reduced.

Thus VMS data have great potential to monitor offshore protected areas. But there remain drawbacks. Not all fishing vessels carry VMS transmitters. They may fall outside size limits, such as those set by the European Union, or they may be registered to nations that do not require their vessels to carry the transmitters. The VMS transmitters may malfunction or even be deliberately disabled so positions are not transmitted even though a vessel is fishing. Other remote sensing approaches may provide a means to overcome these problems and act as 'vessel detection systems' rather than relying on data to be transmitted from a vessel monitoring system. Kourti *et al*. (2005) describe a pilot study using satellite-based synthetic aperture radar to detect vessels at sea even at night and through cloudy skies and concluded that this would be a valuable approach to complement existing fisheries monitoring using surveillance aircraft. For example, in 2004 synthetic aperture radar data revealed the presence of unreported illegal fishing activity in an area closed for haddock conservation near Rockall Bank, northeast Atlantic.

8.2.3 The high seas

The high seas form 64% of the total surface of seas and oceans on Earth and following long-established freedoms of the seas they are beyond any one nation's jurisdiction. The United Nations Convention on the Law of the Sea (UNCLOS, see Topic box 8.1) sets out the framework for national jurisdiction in the oceans. Coastal states have exclusive rights within their 200 nautical mile exclusive economic zones (EEZ) or within the limits of their legally assigned continental shelf (up to a maximum of 350 nautical miles, or 100 nautical miles beyond the 2500 m isobath). Beyond these limits fisheries are governed by a complex system of regional fishery management organisations (RFMOs) that have varying remits in terms of the fish species and portions of the water column they control. Nations that do not sign up to RFMOs are not bound by their conditions and fishing operators can register their vessels with these nations under so-called flags of convenience to avoid high seas fishery controls.

There is now great concern that high seas fish populations have been overexploited and considerable benthic habitat damage has been inflicted by high seas bottom trawling. We run the risk that both fish and benthic ecosystems fall victim to the 'tragedy of the commons' as nations pursue these vulnerable resources exploiting freedoms of the high seas while conservation policy makers struggle to keep up (Berkes *et al*., 2006). As noted earlier, cold-water coral habitats on

Topic box 8.1 **United Nations Convention on the Law of the Sea**

The United Nations Convention on the Law of the Sea (UNCLOS) was established in 1982 and signed into law in 1994 to lay down the rights that nations, both coastal and land-locked, have in the seas and oceans of the world. Subject to international law and other parts of the convention, these rights include freedom to navigate, overfly, lay submarine cables and pipelines, construct artificial islands and other installations, conduct scientific research and fish. This convention gives coastal states exclusive rights to explore mineral resources and benthic species to the limit of their continental shelves (here referring to the political definition of continental shelves as underwater extensions of the continental crust contiguous with the landmass). The convention also lays down obligations to protect and conserve the marine environment, including rare and fragile ecosystems and habitats used by threatened species. In 1994 the International Seabed Authority (ISA) came into being through Part XI of UNCLOS to oversee mineral exploitation on the high seas as part of the 'common heritage of mankind'. The ISA controls seabed exploration and mining outside national jurisdiction and has powers to collect and distribute a mining royalty. In 2000, the UN established a system to discuss ocean issues and improve international co-ordination. This UN Informal Consultative Process on Oceans and Law of the Sea (UNICPOLOS) meets annually and provides a forum for national representatives, international organisations and non-governmental organisations to discuss ocean policy. The UN General Assembly has received reports from UNICPOLOS including discussion of vulnerable marine ecosystem conservation on the high seas (UNEP, 2006).

offshore banks and seamounts show the scars of deep-water bottom trawling. But are deep-water fisheries even economically viable and significant in terms of their role in global food supply? Gianni (2004) estimated that in 2001 high seas bottom trawling represented no more than 0.25% of global marine fisheries as reported by the UN Food and Agriculture Organization. In value, the high seas bottom trawl fishery was equivalent to approximately 0.5% of the global marine fishery total and since these fish were sold predominantly to developed nation markets in Europe, the USA and Japan these fisheries did not contribute significantly to global food security. In a subsequent study using a global catch and landed value database, Sumaila *et al.* (2007) estimated that closing all high seas fisheries would cause a drop in global catches of approximately 9% (although this will be an underestimate because there are significant levels of illegal, unregulated and unreported catches from the high seas). If 20% of the high seas were closed to fishing, Sumaila *et al.* estimated a global catch loss of 1.8% and a global profit loss of US$270 million.

However, taking such profit figures at face value is very misleading. Around the world a variety of government subsidies underpin the agriculture and fishing industries. Khan *et al*. (2006) calculated that the global fishing industry received US$26 billion in the year 2000, excluding fuel subsidies (based on data amassed between 1995 and 2005). Sumaila *et al*. (2006b) estimated the global fuel subsidy was up to an additional US$8.5 billion, or around 25% of the total global US$34.5 billion subsidy. Interestingly, the global profit loss of US$270 million estimated from a 20% high seas closure is less than twice the estimated US$152 million currently paid in subsidies to high seas deep-sea bottom trawlers alone (Sumaila *et al*., 2007). Clearly subsidies at this level will have several consequences. They will dampen the effects of any fuel price increases allowing fishing to continue at great distances offshore when it would otherwise become uneconomic. Since any one nation will be disadvantaged if it unilaterally cuts its subsidy, the only way to lower subsidies and level the economic playing field will be through co-ordinated international action mediated via bodies such as the World Trade Organization (Sumaila & Pauly, 2007).

8.2.4 Stewardship

Much has been written on the ethics of conservation and the factors human society must consider when developing conservation strategy. Our objective here cannot be to review these arguments in detail, but rather to summarise some of their salient features as they relate to cold-water corals and the habitats they form. For discussion of values and ethics in conservation biology see Van Dyke (2003). In the very crudest terms, society will only be motivated to conserve if the object of the conservation effort, be it a landscape, an ecosystem or a species, has some form of value. The total economic value of a natural system, from a landscape to an individual species, can be broken down through broad categories of use and non-use values (Fig. 8.9), outlined in terms of marine resources by Sumaila (2005). But ascribing values to each of these categories is fraught with problems (see discussion in UNEP, 2007), and these problems are greatly magnified when we consider trying to place values on deep-sea ecosystems where our understanding of their basic ecology and functioning is far from complete. Furthermore, this form of cost–benefit analysis shifts the responsibility from those wishing to exploit a system for financial gain and places a duty to ascribe a competing value on those wishing to conserve it.

That said we can attempt to give economic values to cold-water coral habitats. As discussed in Section 5.5, p. 163, some cold-water coral habitats appear important to commercially important fish species, such as gravid female redfish on Norwegian *Lophelia pertusa* reefs. But predicating conservation policy on

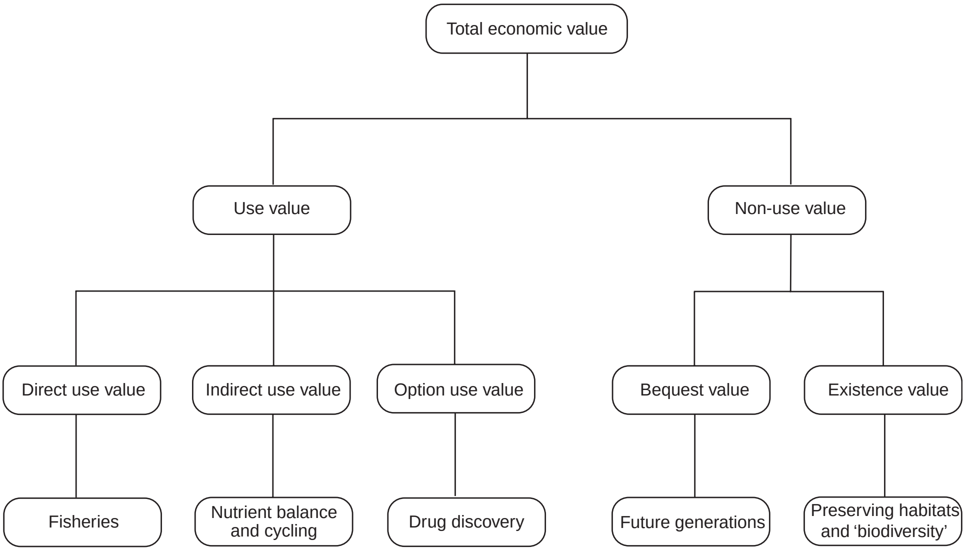


Fig. 8.9. Schematic illustrating the concept of total economic value in the context of benthic biodiversity. Lower level gives examples of potential goods and services provided. Figure adapted from Bateman and Langford (1997) with permission of the Regional Studies Association.

such a value would be a mistake since the redfish, like the vast majority of deep-water fish, are an extremely slow-growing and late maturing group, highly vulnerable to over-exploitation. It is highly doubtful that any deep-sea fishery can be made economically viable (unsubsidised) and sustainable. As time goes on, biomedical research is gradually extracting pharmaceutically active compounds from deep-sea organisms. More than 17 000 compounds have been reported from marine sources and marine biotechnology is a rapidly developing commercial sector. While the majority of compounds described to date come from tropical and temperate species there is now a growing number from cold-water marine organisms (Lebar *et al.*, 2007). Several deep-water sponges have yielded compounds with anti-cancer properties and bamboo coral skeletons show promise as analogues of human bone in grafts (Morgan *et al.*, 2006). Steroids isolated from the cold-water coral *Dendrophyllia cornigera* show cytotoxic activity against human lung cancer cells (Kontiza *et al.*, 2006). It is too early to know whether the highly diverse sponges or other groups found with cold-water corals will yield valuable drugs in the future. However, it is interesting to note that few, if any, would have ascribed economic value to the slimy bacterial films growing by the hot springs in Yellowstone National Park. Yet the heat-resistant enzyme known as *Taq* polymerase extracted from one of these bacterial species forms an essential component of the polymerase chain reaction (see Topic box 2.2, p. 54), a process at the very core of modern molecular genetics and biotechnology industries.

When asked ‘Why should we conserve cold-water corals?’ all these arguments have an important role to play. But perhaps in struggling to ascribe present-day or future economic value to cold-water corals we run the risk of making poor valuations based on incomplete knowledge. In his 1985 paper ‘What is conservation biology?’ Soulé set out four so-called normative postulates to encapsulate the values underlying the ethics of conservation biology: (1) diversity of organisms is good, (2) ecological complexity is good, (3) evolution is good and (4) biotic diversity has intrinsic value. If we take Soulé’s advice then the work described in this book clearly shows that cold-water coral habitats deserve to be conservation priorities. We know that cold-water corals provide habitat to many other species. We know they form highly complex, beautiful structures that have captured the public’s attention making them a poster child for deep-sea conservation movements around the world. We know coral skeletons hold a unique archive of past ocean climate. We know that they have been damaged by bottom trawling and are threatened by climate change. Where there remain doubts, society needs to weigh the short-term benefits of our present-day activities, be they fishing, mining or combustion of fossil fuels, against the loss to future generations of habitats we are only beginning to understand.

In 1992, the United Nations in its Rio Declaration on Environment and Development defined the precautionary principle as follows, ‘Where there are threats of serious or irreversible damage, lack of full scientific certainty shall not be used as a reason for postponing cost-effective measures to prevent environmental degradation.’ We owe it to future generations to conserve and protect the natural world. The intricate and complicated ecosystems of the deep sea, the largest environment on planet Earth, are too often out of sight and out of mind. The scientific community are among the few who have seen cold-water coral habitats and have had the privilege to study them. Researchers, non-governmental organisations and government agencies need to work hard to promote understanding and awareness of these diverse and vulnerable systems so our children and grandchildren may have the same privileges in years to come.

Glossary

Aboral surface	The underside of a coral polyp where it is in contact with the skeleton, see Fig. 3.11.
Abyssal	Pertaining to water depths 2000–6000 m.
Acoustic facies	Grey-scale pattern characteristic of a seafloor type derived from side-scan sonar and multibeam echosounder backscatter data.
Acoustic ground discrimination software (AGDS)	Computer software designed to process acoustic seabed mapping data and identify different seabed types, e.g. sand, exposed rock, coral reef, etc.
Aetiology	The study of why things occur, the study of causes of various phenomena.
Agglutinated	Shell texture characterised by organically bound or biomineralogically cemented components gathered from the ambient environment, e.g. sand grains.
Ahermatypic	Corals that do not contribute to shallow-water reef structure.
Allele	One variation of a gene (one member of a pair) that is located at a specific position on a specific chromosome.
Allelochemical	Substance produced by an organism that is toxic or inhibits the growth of another.
Allochthonous	Originating from outside a system.
Allogenic	Pertaining to an external influence on a system.
Allozyme	Genetically distinct version of an enzyme, see Section 2.6.
Alpha diversity	Number of taxa present within a certain area or ecosystem, see Topic box 5.1.
Amino acid	Basic structural building block of proteins.
Ampullae	Reproductive structures found in hydrozoan corals.
Anastomose	Pattern defining branching and rejoining, used to describe the fusing of branches in some coral types.
Angular unconformity	A buried erosional surface separating two sediment layers. It is angular if the underlying sedimentary units are at an angle to the overlying horizontal sedimentary units.

Anoxia	Lacking oxygen.
Anthozoan	Member of the class of Cnidaria including corals and sea anemones, see Table 2.1.
Antipatharian	Black corals, whip corals, wire corals and thorny corals from the anthozoan order Antipatharia, see Table 2.1.
Antiserum	Medium containing antibodies as a component of the immune system in organisms.
Aphotic	Pertaining to a lack of light.
Aragonite	One of the crystal forms (orthorhombic) of calcium carbonate ($CaCO_3$), see Topic box 4.2.
Aragonite saturation horizon (ASH)	Depth boundary in the ocean between undersaturation and supersaturation of aragonite, below which aragonite goes into solution.
Assay	Procedure to determine concentration.
Authigenic	Formed *in situ*.
Autochthonous	Originating from inside a system.
Autonomous underwater vehicle (AUV)	A pre-programmed, unmanned submarine vehicle useful for mapping and repetitive sampling.
Azooxanthellate	Corals that do not contain endosymbiotic algae (zooxanthellae) but gain nutrients from catching organic particles and prey from the water.
Backscatter	The return (echo) of energy from the seabed to the receiver in an active sonar such as a side-scan sonar or a multibeam echosounder.
Bamboo coral	A type of octocoral (subclass Octocorallia) in the family Isididae, see Table 2.1.
Baseline map	Basic map of the seabed, perhaps showing bathymetry, sediment types and coral reef/carbonate mound locations, onto which more detailed or derived data are overlain.
Bathyal	Pertaining to water depths 200–2000 m.
Bathymetry	The study of ocean depth.
Bedload	Sediment that is transported along the seabed by saltation as opposed to in suspension.
Benthic	Pertaining to the seabed.
Benthic boundary layer	Zone of the seabed/water column interface where the presence of one affects the properties of the other, e.g. where frictional drag from the seabed is evident in the overlying water column.
Beta diversity	Variation in community composition between areas usually measured as the change in taxa between areas, ecosystems or along environmental gradients (‘turnover diversity’), see Topic box 5.1.
Biocalcification	Biologically mediated mineralisation of calcium carbonate, e.g. to form coral skeletons or shells.

Biocoenosis	Assemblage of organisms inhabiting an area of seabed.
Biodiversity	The variety of life, see Topic box 5.1.
Bioerosion	Erosion by organismal activities such as boring, scraping, etching, etc.
Biogenic	Formed by the activity of living organisms.
Bioherm	Body of rock generated by, and composed of, mainly sedentary organisms, e.g. hard corals, calcareous algae or molluscs.
Bioluminescence	Light produced by organisms by the conversion of chemical energy.
Bioturbation	Displacement and mixing of sediment by burrowing organisms.
Box corer	Seabed sampling device capable of retrieving relatively large (often $0.25\,m^2$) samples from the upper 50 cm of the seabed.
Bycatch	Non-target fish or other animals caught in fishing gear.
Byssal threads	Threads used by some bivalves (e.g. mussels) to attach to rocks and other surfaces.
Calcite	One of the crystal forms (trigonal-rhombohedral) of calcium carbonate ($CaCO_3$), see Topic box 4.2.
Calicoblastic cell	Tissue cell responsible for biomineralising calcium carbonate, see Fig. 7.1.
Calicoblastic epithelium	Thin layer of cells (calicoblastic cells) at the base of the stony (hard) corals, which deposits the calcium carbonate skeleton, see Section 7.1.1, p. 211.
Calyx	Skeletal ‘cup’ containing living coral polyp.
Carbon sequestration	Process of storing CO_2 so preventing its release to the atmosphere.
Carbonate platform	Broad, flat, submarine expanse of carbonate rock measuring several hundreds of metres across.
Cementation	Process of binding sediments together by the growth of minerals.
Chalk	Friable limestone formed under relatively deep marine conditions by the accumulation of calcitic coccoliths (from coccolithophorids, pelagic protist algae) specifically from the Late Cretaceous to the Eocene.
Chemoautotrophic endosymbiosis	Situation whereby one organism (symbiont) lives within the body of another (host) and derives energy from the oxidation of inorganic chemicals.
Chemosynthesis	Biological conversion of carbon and nutrients into organic matter from inorganic molecules.
Chitin	A polysaccharide similar to cellulose that serves to strengthen the supporting structures of various invertebrates.
Clade	Group of related organisms that share a common ancestor.

Closed chamber respirometry	Technique to determine the metabolic rate of an organism based on the amount of oxygen consumed in a sealed container.
Cnidarian	Member of the phylum Cnidaria, which includes all corals as well as hydroids, jellyfish and sea anemones, see Table 2.1.
Cnidocyte	Stinging cell characteristic of the Cnidaria, see Section 3.1, p. 68.
Coenenchyme	The tissue-like layer connecting coral polyps. Also known as the coenosarc.
Cold-water coral	Azooxanthellate corals that live in cold and often deep water.
Columella	Central structure of a scleractinian calice (skeletal cup housing the coral polyp) formed by fusion of the inner edges of various septa (radial skeletal plates).
Commensal	Living with another organism (host) but causing no benefit or harm, see Section 5.4.1, p. 160.
Computed tomography (CT) scan	X-ray scan that can be processed to generate a three-dimensional virtual image of the internal structure of an object.
Continental shelf	Shallow water, low gradient submerged extension of continental landmass extending from the coast to the shelf break where slope gradients increase.
Continental shelf break	Deep-water edge of the continental shelf.
Coral carbonate mound	Topographic seafloor structure that has accumulated through successive periods of reef development, sedimentation and (bio)erosion, see Section 4.3, p. 115.
Coral coppice	Dense framework of corals showing vertical zonation.
Coral framework	Coral skeleton of species whose branching morphologies form a complex three-dimensional framework structure.
Coral rubble	Fragments of (bio)eroded coral skeleton.
Coral thicket	Dense association of corals.
Corallum	Complete coral colony.
Cyanobacteria	Blue-green algae that gain energy from sunlight, intermediate between bacteria and higher plants.
Cyclostome	Group of calcareous bryozoans with round zooid apertures.
Cytolytic	Pertaining to cell death by hyperhydration usually resulting in cell rupture.
Cytotoxic	Harmful to the structure and functioning of cells.
Dactylozooid	A specialised hydrozoan polyp adapted for defence and food capture.
Daughter isotope	New isotope of an element following radioactive decay.
Delay signal	Specific characteristics or signature of the complete echo from a sonar.
Dendroid	Possessing a branching structure like a tree.
Deposit feeder	Organism that feeds on organic matter on the seabed.

Diagenesis	Processes of chemical, physical and biological change to sediment after deposition ultimately leading to the formation of rocks.
Diatom	Siliceous single-celled algae and important component of phytoplankton.
Dichotomous key	Key to identifying organisms based on a sequence of yes or no questions about their characteristics, see Figure 3.1.
Dichotomously	Branching into two.
Diel	Occurring on a 24-hour cycle.
Digital map	Map generated from digital data enabling it to be displayed and manipulated on a computer.
Digital terrain model (DTM)	Digital (computer-based) representation of a surface (e.g. ground or seabed topography).
Diploid	Cells that have two paired copies of each chromosome from the mother and father.
Diterpene	Organic compound, group of terpenes ($C_{20}H_{32}$), includes Vitamin A.
Divalent ion	Ion (atom) that has gained or lost two electrons.
Drift deposit	Unit of sediment formed by the progressive accumulation of sediment transported along the seabed.
Dropstone	Isolated rock fragment within finer grained sediment that was dropped to the seabed from a melting iceberg.
Ecology	Study of the interaction between organisms and the environment.
Ecosystem	The relatively self-contained biological community and non-biological environmental factors they interact with.
Ecotoxicology	Study of toxic effects on organisms.
Ectoderm	Outer cell layer of a polyp, also known as the epidermis, see Figure 3.11.
Electrophoresis	Phenomena whereby certain types of particles or molecules dispersed in water will migrate under the influence of an applied electric field.
Endemic	Species that only occur in one geographical area.
Endolithic	Living within a rock.
Endosymbiotic	Organism (symbiont) that lives within the body of another organism (host).
Enzyme	Protein that catalyses biochemical reactions.
Epeiric sea	Broad shallow sea that covers part of a continent.
Epibenthic sledge	Sledge, often mounted with cameras and nets, towed along the seabed.
Epifauna	Animals that live attached to a surface on the seabed.
Ethoxyzolamide	Compound that inhibits carbonic anhydrase.

Eukaryote	Organisms that possess cells containing organelles to perform specific cell functions.
Euphotic zone	Upper layer in the ocean where there is sufficient sunlight for photosynthesis.
Extracellular	Existing outside of the organism.
Facies	A body of rock or a grouping of similar sediments and fossils formed under particular environmental conditions.
Filter feeder	An organism that feeds by straining particles from the water. See also suspension feeder.
Flabellate	Fan-shaped.
Flagelliform	Whip-like.
Floatstone	Limestone with greater than 10% of components larger than 2 mm that are enclosed within finer-grained sediment (matrix-supported), see Topic box 4.1.
Flood basalt provinces	Large volcanic eruption, or series of eruptions, depositing thick, widespread accumulations of basaltic lava.
Food web	Complex network of interactions defining feeding relationships between organisms.
Gamete	Haploid cell that fuses with another gamete during fertilisation in sexually reproducing organisms. Each gamete contains half the genetic information required to make the new (diploid) cell.
Gametogenic	Pertaining to gamete production.
Gas hydrate	Crystalline solid with gas molecules trapped within 'cages' of hydrogen-bonded water molecules.
Gastrozooid	Specialised hydrozoan feeding polyp.
Genotype	Genetic constitution of an organism or individual.
Geochemistry	Study of the chemistry of rocks with techniques applicable to the study of the chemistry of coral skeletons.
Geographic information system (GIS)	Computer system for storing, manipulating and visualising spatially referenced data.
Geological long range inclined asdic (GLORIA)	Long-range side-scan sonar (operated at 100 kHz) used to map large areas of continental shelf in the 1970s and 1980s.
Geophysics	Study of the Earth using quantitative physical methods, e.g. seismics, electromagnetics, radioactivity.
Geotactic	Movement of an organism using the Earth's gravitational field for reference.
Gillnet	Fishing nets of a particular mesh size that trap fish as they attempt to swim through the net.
Glacial moraine	Accumulation of unconsolidated sediment deposited by a glacier.
Global positioning system (GPS)	System used to accurately determine the position of an object on the Earth's surface through triangulation with satellites.

Gonochoric	Organism with two distinct sexes.
Gonophore	Reproductive bud in hydroids.
Gorgonian	Type of coral from the subclass Octocorallia (octocorals), see Table 2.1.
Gorgonin	Complex protein making the horny skeleton of gorgonians.
Grapestone	Limestone composed of aggregated particles.
Ground-truthing	The collection of physical data (e.g. sediment samples, seabed images) to verify interpretations from broader-scale datasets (e.g. geophysical maps).
Habitat	The location or environment where an organism lives, see Section 5.1, p. 144.
Habitat mapping	Plotting the distribution and extent of habitats to create a map.
Hardground	Sediment cemented and exposed at the seafloor.
Hemipelagic	Sediment of mixed terrigenous (land-derived) and biological (planktonic) origin.
Hermatypic	Corals that contribute to shallow-water reef structure.
Heterozygote	Possessing two different alleles for a given gene.
Hiatus	Break in sedimentation without erosion.
Histology	Study of the microscopic anatomy of cells and tissues.
Holocene	Last 10 000 years.
Homoplasy	A character shared by two taxa that has evolved independently and therefore does not imply a common ancestor.
Hydration	Chemical reaction with water, see Topic box 7.1.
Hydraulic theory	Theory that cold-water coral reefs and coral carbonate mound occurrence is related to hydrocarbon seepage, see Section 3.3.1, p. 73.
Hydrocarbon	Organic compound consisting of carbon and hydrogen, used as a general term covering both oil and natural gas fossil fuels.
Hydrocarbon seep	Area of seafloor where hydrocarbons (oil and natural gas) rise out of the seabed.
Hydrodynamic	Relating to the scientific principles describing the motion of fluids and their interaction with solid bodies immersed in them.
Hydrography	Study of the physical characteristics of water.
Hydrothermal vent	Fissure on the seabed through which volcanically heated water issues.
Hydroxylation	Chemical reaction with hydroxide ions (OH^-), see Topic box 7.1.
Hydrozoan	From the class Hydrozoa in the phylum Cnidaria, includes hydroids, hydrocorals, lace corals, stylasterids, fire corals and millepores, see Table 2.1.

Iceberg ploughmarks	Furrows gouged into the seabed by grounded icebergs.
Immuno-cytochemistry	Procedure used to detect antibodies by the presence of specific antigens (that promote antibodies within the cell).
Infauna	Animals that live within the sediment.
Interglacial	Warm climatic period between glacials (ice ages).
Internal wave	Waves that do not oscillate on the surface but within the water, often at the boundary between different water masses.
Interstadial	Warm climatic period within a glacial (ice age) although cooler than interglacials.
Isotope	Different forms of a chemical element with the same number of protons but distinguished by a different number of neutrons.
Kinetic fractionation	Change in isotopic composition as a result of lighter isotopes reacting more readily and so becoming more abundant in the reaction products, see Section 7.1.2, p. 218.
k-strategist	Species adapted to stable environments, usually large with slow development and few offspring per generation.
Landing statistics	Statistics relating to the amount and types of fish offloaded from fishing vessels.
Lazarus taxa	Taxa that appear to become extinct in the fossil record but occur again in later stages. The apparent extinction is often a function of poor preservation and low numbers.
Lecithotrophic	Pertaining to larvae that develop from a large yolky egg.
Lipid	Biochemical molecules including fats, oils, waxes, cholesterol, etc.
Lithic	Pertaining to non-biological sediment or rock components.
Lithification	Process of converting unconsolidated sediment to rock.
Lithoherm	Biogenic mound composed of surface-hardened layers of lithified carbonates.
Longline	Fishing technique using hundreds of baited hooks on a single line.
Macrofauna	Organisms living on or in the seabed whose shortest dimensions are greater than or equal to 0.5 mm, see Topic box 5.2. Also known as macrobenthos.
Manganese nodule	Metalliferous concretions that form slowly on the deep seabed containing high concentrations of iron and manganese as well as other metals.
Marine reserve	Area of seabed legally protected against fishing and other human activities.
Matrix-supported	Rock texture with coarse-grained components surrounded by a finer-grained sediment matrix where the coarse-grained components are not in contact with each other.
Megafauna	Animals large enough to be visible on the seafloor (longer than 2 cm), see Topic box 5.2.

Meiofauna	Infaunal animals passing through a 300–500 µm mesh but retained on a 25–32 µm mesh, see Topic box 5.2.
Mélange	A body of rocks consisting of large blocks of different rock types mixed together.
Mesenteries	Sheets of tissue that form internal divisions in the coral polyp, see Section 3.1, p. 68.
Mesocosm	Artificial environment chamber used in experimentation.
Mesoglea	Gelatinous layer between the ectoderm and endoderm in cnidarians, see Fig. 3.11.
Mesopelagic	Part of the open water column extending from 200–1000 m water depth.
Metagenomic	Pertaining to DNA from organisms in a community when subjected to molecular sequence analyses.
Micrite	Calcareous mud composed of <4 µm long calcite or aragonite crystals, see Topic box 4.1.
Microbialite	Sediment formed under the dominant influence of microorganisms.
Mid-ocean ridge	Submarine volcanic ridge formed at the plate boundary between diverging lithospheric plates.
Milleporidae	Family in the phylum Cnidaria including the fire corals, see Table 2.1.
Mitochondria	Organelle within a cell that generates energy for cellular functions.
Molecular clock	Technique used to estimate when organisms that share a common ancestor diverged, based on the number of molecular differences in DNA sequences.
Molecular evolution	Evolution on the scale of changing DNA, RNA and proteins.
Monophyletic	Descended from a common ancestor.
Multi- or megacorer	Hydraulically damped coring device allowing for almost undisturbed sampling of the sediment–water interface.
Multibeam echosounder	Sonar that produces many accurately navigated soundings across a swath of seabed, see Topic box 1.1.
Nanoplankton	Free floating planktonic organisms 2–20 µm in size.
Niche	Position occupied by an organism in an ecosystem based on its habitat, interactions with other organisms and the environment.
Obligate	Requiring the presence of another species to survive.
Ocean acidification	The process of ongoing decreases in the pH of the oceans due to increasing CO_2 uptake from the atmosphere.
Oceanic productivity	The capacity of the ocean for life.
Octocorallia	Octocorals, subclass of the phylum Cnidaria including soft corals, gorgonians, sea fans, sea whips, sea feathers, precious corals, pink corals, red corals, golden corals, bamboo corals, leather corals, horny corals and sea pens, see Table 2.1.

Oocytes	Female sex cell (gamete) or egg cell.
Ooze	Sediment composed of microscopic biological remains, see Topic box 4.1.
Osmoregulation	Process of controlling the concentration of solutes (osmotic pressure) within body fluids by controlling water and/or salt content.
Otolith	Structure found in the inner ear of fish that contains annual growth rings and hence of use in aging fish.
Packstone	Calcareous mud with larger grains in contact with each other, see Topic box 4.1.
Palaeo-	Pertaining to the past.
Palaeontology	The study of fossils.
Payload	Amount of equipment a vehicle can carry, e.g. sensors on a ROV.
Pelagic	Pertaining to open water.
Petrography	Study of the mineral composition and microstructure of rocks.
pH	Concentration of free hydrogen ions in solution ($-\log_{10} [H^+]$), a measure of acidity and alkalinity, see Topic box 7.1.
Phaceloid coral	Scleractinian (as well as Palaeozoic tabulate and colonial rugose) coral that has skeletal coral cups of uniform height, which are adjoined toward their base.
Photic	Pertaining to light.
Phototactic	Responsive to light.
Phylogeny	The evolutionary relationships among organisms.
Phytodetritus	Plant remains (including dead phytoplankton).
Phytoplankton	Plankton (free floating, drifting organisms) from the plant kingdom dominated by microscopic diatoms and cyanobacteria.
Pinnule	Side-branching structure of the tentacles of soft coral giving them a feathery appearance.
Planktonic	Pertaining to a free floating, drifting lifestyle.
Plate tectonics	The study of the movement of Earth's lithospheric plates.
Pockmark	Large (metres to tens of metres) depression in the seabed caused by the release of sub-surface fluids or gas from the seabed.
Polyp	A single individual of a coral colony.
Polyphyletic	Group of similar species that have evolved from different ancestors.
Precautionary principle	'Where there are threats of serious or irreversible damage, lack of full scientific certainty shall not be used as a reason for postponing cost-effective measures to prevent environmental degradation', see Section 8.2.4, p. 262.
Precious coral	Type of coral skeleton valued as jewellery. Frequently octocorals of the genus *Corallium*, see Table 2.1.

Primary productivity	The transformation of solar energy to biomass via photosynthesis.
Principal component analysis (PCA)	Mathematical technique (vector space transform) used to reduce multidimensional datasets to lower dimensions for analysis.
Prokaryote	Dominantly unicellular organisms that lack organelles within cells. Includes bacteria and Archaea.
Prostaglandin	A fatty acid associated with many biological functions including modifying hormonal effects, muscle contraction and inflammatory reactions.
Proteolytic	Digestion of proteins by cellular enzymes.
Protist	Diverse group of mainly single-cell organisms that are not readily defined as fungi, plants or animals.
Proton	A positively charged sub-atomic particle.
Proxy	A variable that can be measured that mimics another variable of interest allowing it also to be estimated.
Radiation	Increase in speciation, period when the evolution of new life forms is high.
Reef (cold-water coral)	Long-lived, local topographic high that alters local hydrodynamic and sedimentary regimes, whose growth is balanced by (bio)erosion and forms structural habitats for many other species, see Topic box 2.1.
Refugia	Geographic area where isolated populations of once widespread organisms still exist.
Remotely operated vehicle (ROV)	Unmanned submersible remotely controlled from the surface in real-time via a connecting cable. Usually carries cameras, sampling and mapping devices.
Reticulate	Pattern resembling a network.
Ribosomal DNA (rDNA)	Type of DNA present in ribosomes (rather than in the nucleus) involved in protein synthesis.
Ribosome	Complexes of ribosomal DNA and proteins found in cells.
Rugosa	Group of Palaeozoic solitary and colonial corals with a calcitic skeleton. The name refers to their ‘wrinkled’ appearance, see Section 6.1, p. 176.
r-strategist	Species adapted to variable environments, usually showing rapid growth and development with high resource uptake and reproductive rates.
Rudstone	Limestone with >10% components of >2 mm that are in contact with each other, see Topic box 4.1.
Scleractinia	An order of the phylum Cnidaria consisting of organisms with an external aragonitic skeleton and hexamerally arranged body parts. Includes hard corals, stony corals, true corals, cup corals, star corals, solitary corals, zooxanthellate corals and azooxanthellate corals, see Table 2.1.

Scleractiniamorpha	Group of Palaeozoic and Triassic corals regarded as ancestral lineages of the Scleractinia, see Section 6.1, p. 178.
Sclerite	Special structures made of calcitic calcium carbonate found within octocoral tissue. Also referred to as spicules.
Sclerochronology	Study of physical and chemical variations in, and temporal context of, accretionary hard tissues of organisms.
Seamount	Solitary peak extending several hundred metres above the ocean floor. Usually an extinct volcano.
Sediment column	A vertical profile through the seabed from the surface.
Sediment plume	Cloud of suspended sediment.
Sediment trapping	Processes of enhancing sedimentation rates, see Section 4.2, p. 112.
Sedimentary unit	Unit of sediment defined by common properties.
Sedimentation	Process of sediment accumulation.
Seismic artefact	Feature on a seismic image that does not exist in the seabed but is produced by the imaging process.
Seismics	Geophysical method of imaging into the seabed by recording sub-surface reflections of sound waves.
Semidiurnal	Pertaining to half a day or 12 hours.
Septum	Radial skeletal plate that projects into the scleractinian calyx (skeletal cup housing the coral polyp). May be primary, secondary and tertiary structures.
Sessile	Organisms that are stationary or attached, unable to move about.
Side-scan sonar	A geophysical instrument that uses sound waves reflected off the seafloor to map different seafloor types based on the intensity of their echo (backscatter).
Spermatocysts	Tissues producing male sex cells (gametes).
Spicule	Small calcareous or siliceous structures that stiffen and support the tissues of various invertebrates, e.g. sponges.
Stable isotope	Isotopes of elements that do not radioactively decay.
Stereome	Secondary calcareous deposits covering a scleractinian thecal surface.
Steroid	Type of organic compound (polycyclic lipid) involved in many biological functions including role as sex hormones.
Stromatolite	Layered accretionary structures formed by the trapping and binding of sedimentary grains of biofilms formed by microorganisms, especially blue-green algae.
Stylasteridae	Hydrozoan family of the phylum Cnidaria, including lace corals and stylasterids, see Table 2.1.
Submersible	Vehicle able to travel underwater, usually referring to a manned submersible or small submarine.

Substrata	Materials making up the surface on which animals live.
Suspension feeder	An organism that feeds by capturing particles floating in the water. See also filter feeder.
Symbiosis	Relationship between two species of organisms that live together, see Section 5.4.1, p. 160.
Synapticulum	Conical or cylindrical supporting process extending between septa in some scleractinian corals.
Synapticulotheca	Porous thecal wall of dendrophylliids.
Synsedimentary	Occurring at the same time as sediment is accumulating.
Synthetic aperture radar (SAR)	Coherent radar system that generates high-resolution remote sensing imagery using the magnitude and phase of the received signals.
Tabulata	Group of Palaeozoic colonial corals with calcitic skeletons. The name refers to specific skeletal elements, the tabulae, see Section 6.1, p. 176.
Taphocoenosis	An assemblage of organismal remains (fossils) found buried within the seabed.
Taphonomy	Study of how organisms decay and become fossilised, see Section 6.3, p. 193.
Taxonomy	Science of classification, especially referring to the classification of organisms.
Taylor column	Current vortex sometimes found over seamounts.
Thanatacoenosis	An assemblage of organismal remains found on the seabed.
Thecal wall	Calcareous wall of the skeletal cup (calyx) housing the coral polyp.
Thermocline	Layer within the water column showing a pronounced change in temperature with depth.
Thermogenic methane	Ancient methane derived from a deep geological source.
Thermohaline circulation	Density-driven convective circulation system of the world's oceans, see Section 7.3, p. 230.
Three-dimensional seismic data	Closely spaced grid of seismic data that can be interpolated to produce a virtual three-dimensional model of the sub-seafloor.
Towed ocean bottom instrument (TOBI)	A long-range side-scan sonar (operated at 30 kHz).
Trabeculum	Tooth along the upper septal (radial plate in the coral calyx) margin of a scleractinian.
Trace fossil	Preserved evidence of biological activity, e.g. a burrow, footprints, borings.
Transducer	Device that converts electrical energy to acoustic signals and vice versa.
Transponder	A device that receives, amplifies and retransmits a signal.
Trophic	Pertaining to nutrition.
Tuff	Volcanic ash deposit.

Turbidity	Cloudiness of a fluid relating to the density of suspended particles.
Typologies	Data classification based on common traits.
UNICPOLOS	UN Informal Consultative Process on Oceans and Law of the Sea, a forum to discuss ocean policy.
USBL	Ultra-short baseline navigation, system of accurate ship-to-transponder navigation below water.
Ventilation age	Difference in age between the ocean surface and basal water, see Section 7.3, p. 230.
Vital effects	Effects on the isotopic and trace element composition of skeletal material due to biological processes, see Section 7.1.2, p. 218.
Vitellogenesis	Process of depositing nutrients into female gametes or oocytes.
Wackestone	Calcareous mud containing greater than 10% of grains, see Topic box 4.1.
Water column	Vertical profile through the water from the surface to the seabed.
Water mass	Body of water whose physical properties are distinct from surrounding waters.
Xenophyophore	Giant, deep-sea sediment-agglutinating protist measuring up to 25 cm in diameter (e.g. *Syringammina fragilissima*).
Zoanthidea	An order of the phylum Cnidaria including zoanthids and golden corals, see Table 2.1.
Zooid	An individual from a colonial invertebrate animal.
Zooplankton	Plankton (free floating, drifting organisms) from the animal kingdom.
Zooxanthellae	Endosymbiotic dinoflagellate algae (*Symbiodinium*) living within marine invertebrates including corals, sea anemones and giant clams.

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