Chapter 1
Deep-Sea Benthic Habitats

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Abstract

The oceans were observed to be deep during the great age of exploration in the early to mid-nineteenth century. Subsequent exploration demonstrated that the ocean was bisected by underwater mountain ranges and dotted with abyssal hills. With the advent of the echosounder and latterly multichannel swath bathymetry, we now know that the deep ocean has topography as diverse as found on land. In the last 30 years, with an increase in deep-sea scientific activity and the use of underwater vehicles, we have learned that the deep sea consists of a series of habitats and ecosystems interconnected by hydrography and topography. The more recent challenges have been how to sample and analyse these separate habitats and ecosystems. This chapter describes the different environments and briefly outlines the main methods of sampling for each habitat or ecosystem. More detailed aspects of these sampling methods are found in subsequent chapters.

Keywords   sampling, continental slope, canyon, cold-water coral reef, cold seep, mud volcano, mid-ocean ridge, hydrothermal vent, abyssal plain, trench, seamount

1.1   Introduction

Since the great age of oceanic exploration sailors have recognized that the oceans get deeper as their ships move away from the coast. The abruptness of this increase in depth was known to vary throughout the global ocean, with extensive shallow shelves off some coastlines, such as northwestern Europe, and precipitous increases in depth close to shore in other areas, as seen in the southeastern Pacific. In an age of cast lines to determine depth, data on oceanic depths was limited and accumulated slowly; it was only when there was a technology imperative, such as the seabed survey by HMS *Cyclops* in the North Atlantic prior to the laying of the first transatlantic telegraph cable in 1857, that our knowledge increased. This survey demonstrated that, on leaving Europe, the cable would cross the continental shelf, sink across the continental slope and cover most of its distance across the Atlantic on abyssal plains at depths greater than 5000 m (Murray & Hjort, 1912). However, the great depth of the Atlantic appeared to be bisected by a linear structure we now call the Mid-Atlantic Ridge that forms an element in a submarine mountain chain that circles the globe. These 'primitive' methods of sounding continued well into the twentieth century, so our knowledge of the ocean seafloor was composed of spot depths on naval charts.

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The advent of the echosounder in the 1930s gave a continuous record of the depth of the seabed traversed, and increased the resolution of depth measurements considerably. It was the compilation of all the data to date in the early 1960s that gave rise to the iconic seafloor figure produced by Bruce Heezen and Marie Tharpe, which integrated for the first time depth measurements into a single three-dimensional figure. And what a figure this turned out to be. This and subsequent maps of the world's seafloor revealed that the oceans were more complicated than simple deep basins covering ~70% of the surface of the Earth (Fig. 1.1). The most prominent features were apparently flat plains between 3 and 6 km depth that cover 50% of the surface of the Earth (Figs 1.1 and 1.2).
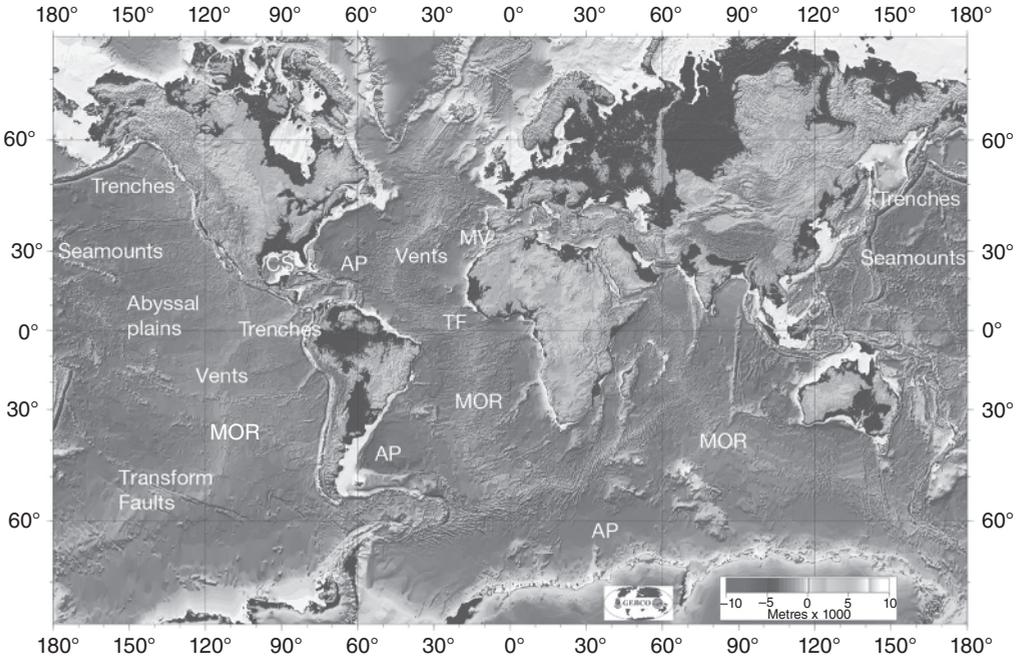
Fig. 1.1   Bathymetry of the global ocean showing a selection of the main features. MOR, mid-ocean ridge; AP, abyssal plain; TF, transform faults; MV, mud volcanoes.
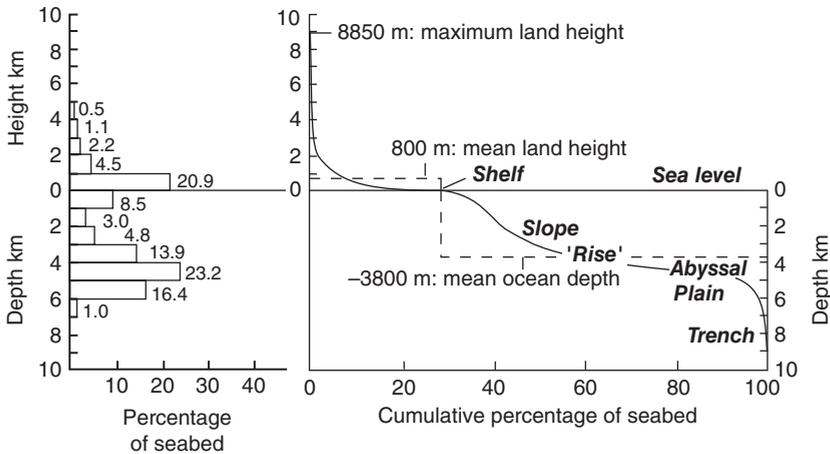
Fig. 1.2   Hypsographic curve of the percentage of the global ocean at 1000 m depth intervals.

In many places, these plains were not only separated by submarine mountain ranges but were pock-marked by individual mountains or groups of mountains now termed seamounts. Particularly obvious in the Pacific was a series of very deep linear basins referred to as trenches, which are now known to occupy only 1% of the ocean but extend to the greatest depths of just short of 11 000 m. As we zoom in on the seabed topography, we see a steep slope between the shallow continental shelf and ocean basin referred to as the continental slope, the sediment-draped base being called the continental 'rise' or 'fan', although there is some dispute about this terminology. From the 1990s, widespread use of precise satellite navigation and a new generation of multibeam echosounders producing 3D swath images of the sea floor (Fig. 1.3) revealed further details. The continental slope may be smooth or bisected by submarine canyons that, at first glance, appear as gashes normal to the submarine contours. The continental slope is also a major site for cold seeps, one of the forms of chemosynthetically driven ecosystems now discovered, particularly in sedimentary areas. A similarly functional ecosystem is found along the mid-ocean ridges (MORs) and other volcanic areas, such as back-arc basins and subduction zones. Here, hydrothermal vents, so-termed owing to the expulsion of hot fluid, rich in sulfide, methane and dissolved minerals, support abundant local communities. Related faunal communities are found on even more localized habitats, such as whale falls and other organic inputs such as wood and kelp (at a scale of metres) that form their own ephemeral ecosystem on the seabed.

It is the scale variation from thousands of kilometres on abyssal plains or along mid-ocean ridges to the small decimetre scale of vents and organic falls, together with the type of substratum, whether sedimentary, rock or biogenous, that drives the different sampling strategies employed to understand deep-sea ecosystems. It is only in the last 20 years or so that we have truly resolved the deep sea into its component ecosystems. Although available information is still limited and we do not know the exact extension of most of these ecosystems, deep-sea research has greatly developed in the last decades (Danovaro *et al.*, 2015; Ramirez-Llodra *et al.*, 2010a).

We will now describe the main features that will define sampling strategies for these different systems. Our approach is to examine the deep sea by moving out from the shore over the continental
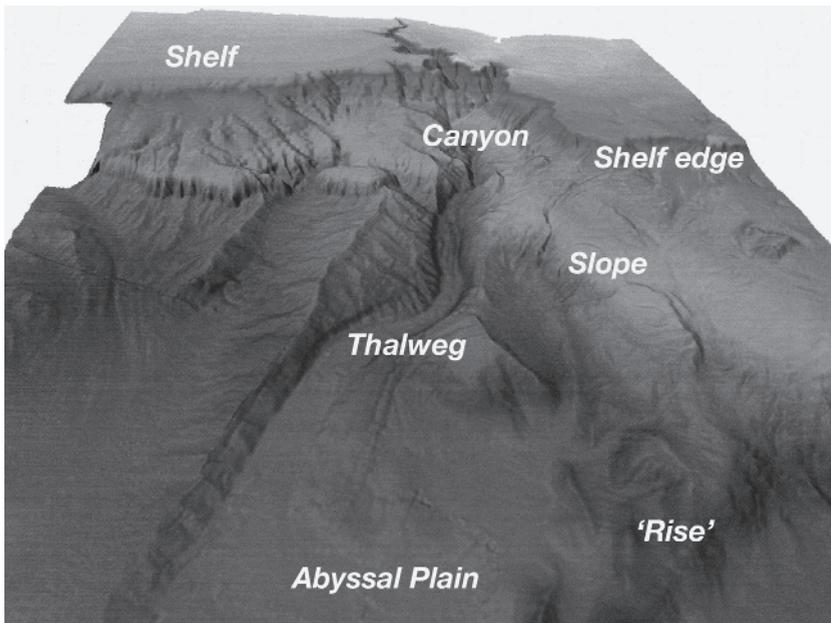
Fig. 1.3   Three-dimensional image of the Nazaré submarine canyon and nearby continental slope off the coast of Portugal showing the main features of the continental slope and a canyon. The view is to the east from open ocean.

shelf and margin, out over the abyssal plains to reach the MOR systems and eventually the trenches or subduction zones. Embedded in these global scale features are smaller scale habitats such as cold-water coral reefs, canyons, seamounts, cold seeps and hydrothermal vents. We will define each habitat, examine the main sampling methodologies and discuss their limitations (Table 1.1).

1.2   Ecosystem and habitat diversity in the deep sea

1.2.1   Moving into deep water

Although we now recognize different ecosystems and habitats within the deep sea, it is essential to acknowledge that they are all interlinked *inter alia* through hydrography in the water column, primary productivity arising from vertical flux of surface production or microbially mediated chemosynthesis and variation in the composition of the seabed from soft sediments to rocky outcrops.

As we move away from shore, the seabed sinks gently to a depth of 200 m. This is the continental shelf (Figs. 1.2 and 1.3) that provides most of the current ecosystem services from the ocean. In Antarctica the shelf occupy depths down to ~600 m as a result of the weight of the icecap on the surrounding continent. Throughout the world, the edge of the continental shelf is defined by an increase in the angle of the seabed (the shelf edge) (Fig. 1.3) and from this point down to depths of ~3000 m we find the continental slope (Figs 1.2 and 1.3). Together these are referred to as the continental margin and represent the most diverse collections of habitats in the ocean (Menot *et al.*, 2010), including soft sediment slopes, canyons, cold seeps, cold-water corals and brine pools.

Continental slopes vary throughout the global ocean, mainly determined by whether they are passive or active margins. Bordering Europe, the eastern United States, eastern South America, all Africa and Australia, margins are passive and extend for thousands of kilometres. In many cases the continental slope increases in depth at an angle of about 8° (equivalent to the relatively gentle slope on a hillside). Although rock outcrops may be present, most of the slope is covered with sediment (Fig. 1.4a) and at the base of these slopes there is a decrease in the angle, giving rise to the continental deep-sea fan (or rise). In certain conditions where there has been a catastrophic influx of sediment into the deep sea by turbidity currents (Talling *et al.*, 2007), there is the formation of a more specialized sedimentary feature called a turbidite. Along active margins, such as off the west coast of North and South America, the continental slope plunges straight down to the adjacent trench and has no obvious continental fan. The sedimentary environments of the continental slope and fan (especially on passive margins, although not turbidites) give rise to some of the highest biodiversity in the deep sea (Grassle & Maciolek, 1992). Since the nineteenth century, the traditional methods of sampling these areas have included trawls, sleds and box-corers, and these methods are still widely used today (Table 1.1), although they have been supplemented by the use of submersibles and remotely operated vehicles (ROVs) for small-scale work and autonomous underwater vehicles (AUVs) for wider scale surveys.

Not all margins follow this simple pattern and it is the heterogeneity of environments that leads to the apparent high species diversity found at these bathyal depths between 200 and 3000 m (Levin *et al.*, 2010). Where the continental slope is steep enough to prevent settlement of sediment and bedrock forming, the margin is exposed (Tyler & Zibrowius, 1992). Hard substrata also occur at higher latitudes in all oceans where drop stones from melting icebergs, both past and present, increase the local heterogeneity of the seabed. Such drop stones interact with the local hydrography, modifying the sedimentology of the immediately adjacent seabed (Fig. 1.4b). In such a situation, sessile attached megafauna may be found, which are not easily sampled other than by the use of submersibles or ROVs (Tyler & Zibrowius, 1992). The ripples and winnowed sediment observed in Figure 1.4 are evidence of current flow along the contours of the continental slope.

Table 1.1 A summary of the main deep-sea habitats, their definitions, and the types of sampling methods, as well as the main considerations for each method

Habitat	Definition	Sampling methods	Sampling considerations
Continental shelf	The seabed between low water spring tide and the shelf edge usually at ~200 m depth (deeper on the Antarctic continental shelf)	Trawls, sledges, grabs, corers, drop and towed cameras	Often well sampled or fished so data may be biased by past sampling/exploitation
Continental slope	From about 200 m depth where there is an increase in gradient down to ~3000 m depth)	Trawls, sledges, grabs, corers, submersible, ROV, epibenthic sledges, drop and towed cameras, landers	Generally straightforward to sample except in very steep and/or rocky areas
Submarine canyons	Irregular fissure-like incisions in the continental slope crossing the depth contours from 50 m to >4000 m	Submersible, ROV, drop cameras; in well-known canyons trawls, epibenthic sledges, towed cameras and corers have been used	Steep-sided and narrow and difficult for trawls and accurate coring
Cold-water coral reefs	Ahermatypic corals that form reefs down to 2000 m depth, the most common species being *Lophelia pertusa*	Submersible, ROV, towed cameras	Delicate structure vulnerable to disturbance or destruction by trawls, epibenthic sleds etc.
Cold seeps	Sedimentary chemosynthetic ecosystems fuelled by thermogenic or biogenic methane and/or hydrogen sulfide	Corers, drop and towed cameras, submersible, ROV	Small spatial extent
Oxygen-minimum zones	Zones along the continental slope where the water column oxygen-minimum zone impinges and results in low oxygen values close to the seabed	Corers, trawls epibenthic sledges, drop and towed cameras, ROV	Often 'soupy' consistency of surface sediment that makes trawling and coring difficult
Mud volcanoes	A form of cold seep looking like a 'cow pat' that often exudes fluid mud	Drop and towed cameras, corers, submersible, ROV	Small spatial extent
Methane hydrates	Methane held in a water matrix under particular temperature/pressure condition forming a solid	Submersible, ROV	Small spatial extent if exposed at the seabed at all
Pock marks	'Holes' in the sediment on various scales caused by burrowing fauna or geological movement	Submersible, ROV	Small spatial extent
Deep-sea fan	Sedimentary area where the incline of the continental slope decreases and ultimately merges with the abyssal plain, composed of alluvial sediment	Trawls, epibenthic sledges, corers, drop and towed cameras, ROV	The presence of turbidites results in sediment heterogeneity over a wide range of scales

Table 1.1 (Continued)

Habitat	Definition	Sampling methods	Sampling considerations
Abyssal plains	The extensive 'flat' sedimentary seabed between 3000 and 6000 m deep	Trawls, epibenthic sledges, corers, ROV, AUV, drop and towed cameras, landers	Shows spatial heterogeneity on a variety of scales from kilometres to centimetres. Small, soft-bodied forms dominate
Hypersaline pools	High-salinity anoxic small-scale habitats found at abyssal depths	ROV	Small spatial extent, anoxic, very limited metazoan fauna
Seamounts and guyots	Seamounts are usually extinct volcanoes that rise hundreds or thousands of metres above the surrounding seafloor. Guyots are flat-topped seamounts	Submersible, ROV, drop and towed cameras, epibenthic sledges, corers	Steep sides, mostly hard and rugged substrate (apart from top of guyots where sediment accumulates). Can have delicate fauna vulnerable to disturbance from trawl, sled sampling
Mid-ocean ridge including transform faults	The 60 000 km ridge system, also called the 'spreading centre', often down the centre or off-centre in the main oceans. Transform faults are large 'slashes' in the MOR	Submersible, ROV, trawls	Mainly a rock fauna and often very sparse
Hydrothermal vents	Chemosynthetically driven ecosystems fuelled by hydrogen sulfide formed by water/rock interactions at specific sites along the MOR and back-arc volcanoes and basins	Submersible, ROV, AUV, drop and towed cameras	Small spatial extent, and some sites have a short 'life' span. High biomass. Some delicate communities that would be disturbed by destructive gears
Trenches	Found along active margins where one plate subducts below another plate to form the deepest parts of the ocean from 6 km to 11 km depth	Trawls, landers, ROV	Very deep and a long time to collect each sample
Organic food falls	Whale falls, wood falls and macroalgal and seagrass falls	Submersible, ROV, towed cameras and landers	Very small spatial extent and limited 'life' span

Continental margins can also be impacted by oxygen-minimum zones (OMZs) (Levin, 2003). These zones occur at bathyal depths, particularly in the eastern Pacific and the Arabian Sea, where sinking organic matter from high surface production is remineralized, with heterotrophic bacteria stripping the water column of oxygen. Where the OMZs impinge on the continental slope, the fauna at the seabed tends to have reduced diversity, although some species are adapted to hypoxic conditions (Creasey *et al.*, 1997). There is no special sampling strategy for OMZs, although sampling of
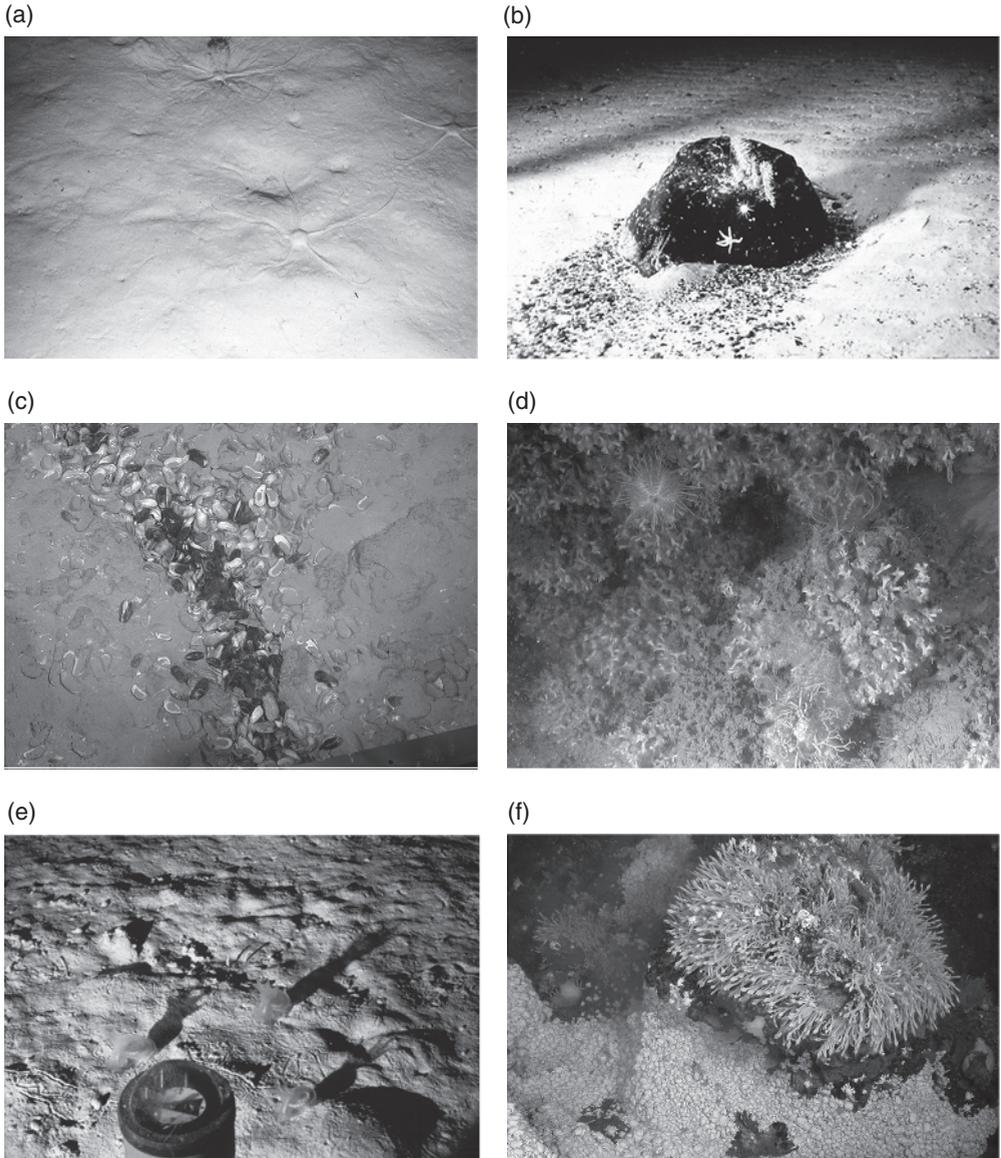
Fig. 1.4 (a) The continental slope seabed at 2200 m depth in the Northeast Atlantic showing ophiuroids on foraminifera ooze. (Photograph by P.A. Tyler.) (b) A drop stone in the continental slope at 2639 m in the Northeast Atlantic showing the winnowing of sediment downstream of the drop stone and current generated ripples in the background. (Photograph by P.A. Tyler.) (c) *Bathymodiolus mauritanicus* alive and dead on the Darwin mud volcano at 1100 m depth. (Photograph courtesy of NOC/NERC. Reproduced with permission.) (d) The frame-building cold-water coral *Lophelia pertusa* in the Whittard submarine canyon at 1300 m depth in the Northeast Atlantic. (Photograph courtesy of NOC/NERC. Reproduced with permission.) (e) The Porcupine Abyssal Plain at 4800 m in the Northeast Atlantic showing tracks, trails and pits in which phytodetritus can accumulate. The small holothurian is *Amperima rosea*. (Photograph courtesy of DSM Billett NOC/NERC. Reproduced with permission.) (f) Dense populations of the yeti crab *Kiwa tyleri* and the barnacle *Vulcanolepas* sp. at hydrothermal vents along the southern part of the East Scotia Ridge, Antarctica, 2500 m depth. (Photograph by ChEsSo consortium.) (Please see Plate 1 for colour representation of the figure.)

the water column and interstitial salinity from sedimentary cores become important. The use of perspex cores in a megacore allows visual examination of the cores to show the various layers of change down the upper sedimentary column.

The apparent 'smoothness' of the continental slope is bisected in many areas of the global ocean by submarine canyons. These arise close to the shelf edge or part way across the shelf and form a deep chasm normal to the contours of the slope (Fig. 1.3). Canyons are subjected to specific geo-chemical, hydrographic and sedimentological processes (Canals *et al.*, 2013) that enhance organic matter transport (Puig *et al.*, 2003) and shape faunal community composition and structure (Ramirez-Llodra *et al.*, 2010b; Schlacher *et al.*, 2010). The formation of submarine canyons has led to much debate, whilst the environmental conditions within canyons such as strong currents and turbidity flows have hindered their study. Deployed equipment, such as current meters, can be swept away and lowered corers may be difficult to position where intended (Canals *et al.*, 2006). Trawls are invaria-bly lost, except in canyons where the topography is particularly well known. The most successful recent studies of canyons have employed ROVs (Huvenne *et al.*, 2011), but still the use of such powered vehicles present challenges even in moderate currents with suspended sediments in canyons (Tyler *et al.*, 2009). A second major problem for canyon analysis studies is the extreme heterogeneity (of depth, substratum type, seabed morphology, etc.) at different scales from thousands of kilometres down to metres where seabed type and depth may vary, whereas currents and suspended sediment load may vary on a tidal time scale.

Another feature of the continental margin are cold seeps (Sibuet & Olu-Le Roy, 2002; Levin, 2003). Cold seeps are environments where biogenic or thermogenic methane and biologically mediated hydrogen sulfide form the basis for primary production for the local food web (Tunnicliffe *et al.*, 2003). The name of the environment derives from the seepage of these compounds in the sediment and that there is no increase in temperature (Levin, 2003). One of the most common forms of cold seep is the mud volcano, of which classic examples occur in the Gulf of Mexico, Barents Sea (Haakon Mosby Mud Volcano), Mediterranean Sea and the Gulf of Cadiz (Fig. 1.4c) (Olu-Le Roy *et al.*, 2004; Vanreusel *et al.*, 2008). Mud volcanoes look like the classic 'cow pat' and can be 100–200 m diameter. Infrequently mud pours out of the mud volcano and forms a slide down the flank of the volcano. Typical macrofauna include siboglinid tubeworms and bathymodi-olid mussels (Fig. 1.4c) as found at hydrothermal vents. In addition, some mud volcanoes support colonies of octocorals, presumably feeding on the local bacterial production (Levin, 2005). On passive margins are found 'pock marks' (Ondréas *et al.*, 2005; Olu-Le Roy *et al.*, 2007). Pock marks are conical dips in the seabed sediment that often have associated seeps because of gas loss. In the Gulf of Mexico, a highly specialized form of cold seep is the 'brine pool' (MacDonald *et al.*, 1990). This pool is some 30 m long and contains water at 120 ppt salinity. At the base of the pool is a salt dome and arising through the waters of the pool and the surrounding sediment is methane that fuels the methanogenic bacteria endosymbiotic with the mussel *Bathymodiolus childressi*. This mussel bed has a distinct fauna that contribute to the local diversity. Other small forms of cold seep are methane hydrates that appear to support an endemic species, the ice worm *Hesiocaeca methanicola* (MacDonald *et al.*, 2003). Another highly specialized type of cold seep are the Campeche asphalt volcanoes found in the southwest Gulf of Mexico (MacDonald *et al.*, 2004). These are unique habitats characterized by the episodic intrusions of semi-solid hydrocarbons that spread over and form structures with a significant vertical relief: the Chapapote knolls. Finally, one of the most recently discovered novel forms of seepage are the 'hydrothermal seeps'. These hybrid systems, where methane seepage and diffuse hydrothermal flow are found together, have been documented along the Costa Rica margin (Levin *et al.*, 2012).

Cold seeps, mud volcanoes, pock marks and other such features present their own sampling chal-lenges. In most cases they are relatively small and, although sedimentary, they are not easily sampled by corer from surface ships. The most successful programmes for the analysis of cold seeps have involved the use of visual observation, faunal sampling and coring from submersibles and ROVs.

A final specialized environment of the continental margin is that of cold-water coral reefs (Freiwald, 2002). Most people are familiar with tropical shallow water reefs, the corals of which rely on symbiotic zooxanthellae for the deposition of calcium carbonate. Typically at bathyal depths in the ocean, there is a suite of corals that are azooxanthellate (having no zooxanthellae) but are successful in building reefs. The best known of these corals is *Lophelia pertusa* (Fig. 1.4d), but they also include the coral genera *Oculina*, *Madrepora* and *Solenosmilia*. These corals are 'frame builders', the frame being calcium deposited by the coral. The interstices of the frames provide a habitat for a wealth of invertebrate fauna and fish, making them an exceptionally high biodiverse environment. These reefs may be found throughout the global ocean but are particularly common in the North Atlantic (Zibrowius, 1985; Mortensen *et al.*, 2008; Davies *et al.*, 2008). They are especially vulnerable to deep-sea fishing where the corals are destroyed by the nets of heavy fishing gear that may clear an area of its corals and all the associated fauna (Hall-Spencer *et al.*, 2002). Cold-water corals present difficulties for sampling in both practical and legal terms (e.g. some deep coral reefs are protected from disturbance and only non-destructive scientific sampling is allowed). Today, the main sampling effort is by the use of ROVs, but cold-water corals may also be surveyed by side-scan sonar, towed cameras and the use of AUVs.

1.2.2   *The most extensive benthic environment on Earth*

As we reach the bottom of the continental slope, the seabed starts to level off and between 3000 and 6000 m depth we have the most extensive benthic environment on Earth: the abyssal plains. These plains cover 50% of the total Earth surface (Fig. 1.2) and, although they vary depth and contain both basins and hills on a scale of kilometres, their slope is imperceptible. All the oceans of the globe have abyssal plains (Fig. 1.1). The original perception was that they were flat and featureless and, when viewed by low-resolution multibeam swath bathymetry from a surface vessel, this may appear to be the case. The traditional method for sampling the abyssal plains has been the use of trawls and sleds for larger fauna, box-corers for macrofauna, and multicores for meiofauna. Photography gives an *in situ* view of the seabed and it was soon realized that, although flat, there was considerable heterogeneity within this mainly sedimentary environment (Fig. 1.4e). Simply, there are bumps and dips often at the sub-metre scale. The bumps may be mounds formed by burrowing organisms living in the sediment and close examination shows that this disturbance affects the local biodiversity. Tracks and trails also create very small-scale disturbance that can lead to heterogeneity on the sub-metre scale. Dips in the seabed often get filled with phytodetritus from surface production, which has sunk to the seabed and collected in these hollows. In the Pacific, manganese nodules are scattered on the abyssal plain and form their own unique 'province', with the manganese nodules supporting a fauna composed mainly of foraminifera (Mullineaux, 1987; Miljutina *et al.*, 2010). In the Mediterranean Sea, anoxic hypersaline pools have been found at abyssal depths (van der Wielen *et al.*, 2005). Such environments were thought to be the preserve of microorganisms only, but Danovaro *et al.* (2010) have shown that at least three new species of the phylum Loricifera are capable of living under these conditions.

This habitat variation on the extensive abyssal plains leads to high diversity but low biomass amongst small infauna, including polychaetes, nematodes and peracarid crustaceans (Vanreusel *et al.*, 1995; Lambshead *et al.*, 2001; Brandt *et al.*, 2007; Levin *et al.*, 2010) although biomass is low as a result of low food availability (Smith *et al.*, 2008). Thus the problem for sampling abyssal plains is that, by trawling over a couple of kilometres of seabed, the trawl will integrate the diversity of the seabed, whereas coring or sampling by submersible or ROV will differentiate the biodiversity on a micro-scale. Mosaicking from ROVs is developing as a tool to examine the sub-metre scale variation on abyssal plains.

Although extensive, the abyssal plains may be dotted, or even peppered as in the Pacific, by seamounts. There is a very specific definition that states seamounts are volcanoes, usually extinct, that rise hundreds or thousands of metres above the surrounding seafloor (Koslow, 2007; Pitcher *et al.*, 2007) (Fig. 1.5). They are formed at MORs and are carried across the floor of the ocean by tectonic
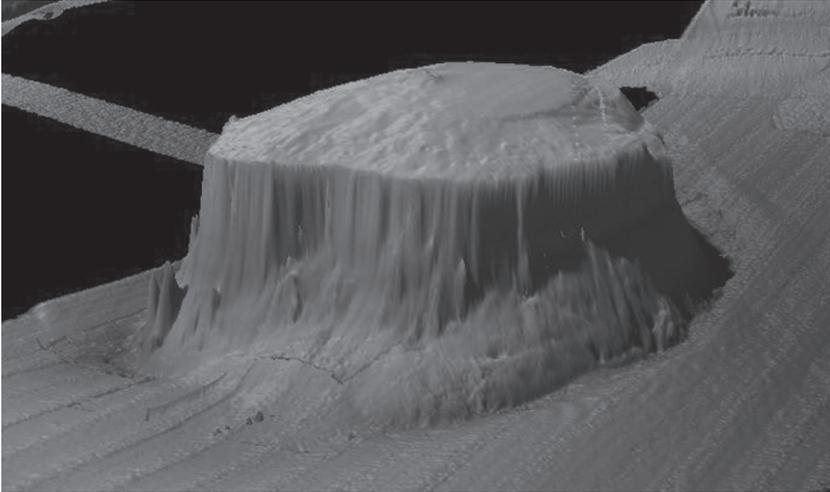
Fig. 1.5   Swath bathymetry of the Anton Dohrn seamount with its flat top, technically a guyot. (Image courtesy of Colin Jacobs, NOC.)

plate movement. This is seen particularly elegantly in the Emperor seamount chain formed by the Pacific hotspot that is now creating the Big Island of Hawaii. As these islands are moved to the north-west, they are eroded away to below sea level to form seamounts or guyots (where the top of the seamount is particularly flat, as in the Anton Dohrn seamount in the Northeast Atlantic (Fig. 1.5)). All seamounts are steep sided and their shape modifies the flow past them, with flow accelerating near the summit (Genin *et al.*, 1986). Because of the steep sides and the accelerated flow over sea-mounts, the associated fauna is often sessile and filter feeding and includes a high abundance of all types of coral (Clark *et al.*, 2010). Such an environment, as with cold-water coral reefs, attracts a high invertebrate and vertebrate diversity. This, together with the trapping of vertically migrating pelagic organisms, makes seamounts potentially intense fishing grounds and some seamounts in the global ocean have been devastated by deep-water fishing (Rogers, 1999; Althaus *et al.*, 2009).

An additional stress on seamounts is when the top of the seamount protrudes into the OMZ, which results in a natural reduction in biodiversity over the top of the seamount (Wishner *et al.*, 1990). As with many of these specialized environments in the deep sea, traditional sampling methods have limitations, and submersible technology is often the preferred way of studying seamounts, although cameras towed from surface vessels have been used successfully (e.g. Rowden *et al.*, 2010).

1.2.3   Mountain chains and hot fluid

The abyssal plains do not extend from continent to continent. As one moves across the ocean, there is a decrease in water depth, an increase in the ruggedness of the terrain and an increase in the proportion of rock at the seabed. This is the foothills of the MOR (Fig. 1.1), a 60 000-km-long structure that runs along all oceans. The MOR is the site of formation of new ocean floor. As the ocean plates are dragged down into the subduction zones, new seafloor material is added at the MORs. Mid-ocean is a bit of a misnomer, as these 'spreading centres' are roughly mid-ocean in the Atlantic and Indian oceans but are asymmetrically offset to the east in the Pacific (Fig. 1.1). The correct term should be spreading centres, but MOR is in common use. We know very little about the environment of MORs except for hydrothermal vents. The cross-section of the MOR can vary from a deep summit axial graben of 1000 m (as seen in the Atlantic) to the very shallow axial valley seen along the East Pacific Rise (Van Dover, 2000). More distinctive features of the MORs are the transform faults (Fig. 1.1) that appear as giant

slits at right angles to the main axis of the ridge. These transform faults allow deep circulation between the deep basins either side of the MOR and may prove to be important conduits of reproductive propagules between the different ocean basins. Although of great linear extension, the MOR has not been sampled extensively, although the MAR-ECO and ECOMAR projects have examined the Mid-Atlantic Ridge close to the Charlie–Gibbs Fracture Zone (Bergstad *et al.*, 2008). Remarkably, they were able to trawl areas of the ridge as well as using corers, submersibles and ROVs.

A distinctive feature of spreading centres are the hydrothermal vents. These were first discovered in 1977, when geophysicists could not explain the heat loss of the Earth's interior by conductive heat loss alone, citing the expected presence of convective heat loss. Along the Galapagos Rift, they found the predicted convective heat loss and serendipitously discovered what became known as the hydrothermal vent fauna (Corliss *et al.*, 1979). A hydrothermal vent occurs when seawater has percolated through the oceanic crust, reacted with the subsurface rock, been heated by magma and had its chemical composition changed by removing all oxygen and magnesium, reducing sulfate to sulfide and incorporating metals. The water released at the hydrothermal vent is rich in hydrogen sulfide, which reacts with seawater to precipitate as sulfide (Van Dover, 2000; Tolstoy *et al.*, 2008). The formation of the chimney from which hydrothermal fluid emanates varies in structure and may affect the distribution of local fauna. In the Northeast Pacific, 'flanges' control the escape of vent fluid, leading to the strongest thermal gradient on Earth, whilst in some Atlantic vents 'beehive diffusers' are found (Van Dover, 2000). The hydrogen sulfide provides an energy source for microbially mediated primary production by chemolithoautotrophic microorganisms found both free living, forming bacterial mats, and as endosymbionts in certain endemic vent species (Childress & Fisher, 1992). This metazoan fauna, although of relatively low biodiversity, produce a magnificently high biomass of fauna at the vent, surrounded by the very low biomass of the adjacent deep sea (Fig. 1.4f). Hydrothermal vents are also found at subduction zones as well as spreading centres.

The discovery of vents changed the basic paradigms of marine biology for ever. However, sampling and studying of vents could only ever have been carried out by the use of submersibles and more recently ROVs, as the scale at which the sampling takes place is sub-metre and even at centimetre scale.

1.2.4   *Into hades*

At the other end of oceanic plates, destruction takes places in a subduction zone where, usually, the heavier oceanic plate subducts beneath the lighter continental plate (Fig. 1.1). Because both plates are sinking, we find the deepest ocean on Earth, the trenches, between 6000 and 11 000 m, the best examples of which are found in the western Pacific (Fig. 1.1). Trenches occupy only 1% of the globe and by their tectonic morphology are both deep and very linear. Trenches were first sampled only in the early 1950s by the Danish *Galathea* and Russian *Vitjaz* expeditions that used trawls (Jamieson *et al.*, 2010). Piccard and Walsh dived into the Marianas Trench in 1960 in the bathyscaphe *Trieste*, but after only a brief glimpse of the deepest point on Earth, they dropped their ballast and rose back to the surface. The only other dive to the deepest point on Earth was made in 2012 by James Cameron, who piloted solo the DEEPSEA CHALLENGER submersible. So far, we know that trenches support high bacterial abundance and biomass (Danovaro *et al.*, 2003), as well as an important and diversified benthic fauna (Belyaev, 1989). Sibuet *et al.* (1988) have also reported the existence of a cold seep fauna in the upper parts of the subduction zone off Japan, and Fujikura *et al.* (1999) reported the deepest recorded seep at over 7000 m in the Japan Trench.

New technology of sampling such depths is now available and are permitting exciting investigations of the hadal environment. Hybrid remote vehicles are coming on line to be able to sample such environments routinely. Two deep-sea robotic vehicles, *Nereus* (USA) and *Kaiko* (Japan), have already reached the deepest parts of the Marianas Trench. To date, some of the most successful sampling has been with landers equipped with baited cameras and traps that have identified taxa not thought to occur at hadal depths (Jamieson *et al.*, 2009).

1.2.5 Special cases

The habitats and ecosystems described above are geographically determined by the tectonic activity or history of the great tectonic plates. There are, however, a number of 'minor' ecosystems that are not necessarily geographically determined. These include whale and wood falls as well as seagrass and algal clumps. Generally, these ecosystems are transient, although there is evidence that whale falls may have an impact on the seabed that lasts decades (Smith & Baco, 2003). The main effect of these mini ecosystems is to increase local biomass, although local species diversity immediately adjacent to the organic input may decrease and cause local chemosynthetic activity, particularly in the sediments (Bernardino *et al.*, 2010; Smith & Baco, 2003). There has also been the implication that these 'minor' ecosystems are important stepping stones for the dispersal of reproductive propagules throughout the deep sea (Distel *et al.*, 2000). Because of their small scale, these organic inputs can only be examined by the use of submersibles or ROVs.

1.3   Conclusions

Sampling of the deep seabed has changed considerably since the heroic age of deep-sea exploration. The pioneers used trawls and dredges which sampled relatively flat surfaces of sediment or rock. In the 1960s, a move to quantitative determination of the biodiversity of the deep sea led to the development of quantitative samplers, the USNEL box-corer being the workhorse for some 40 years, only recently being replaced by the megacorer. Such corers were limited to sedimentary seabeds and still caused disturbance as they landed. Technology has helped dampen this effect but not eliminated it. The scale of sampling ability was also reduced to sub-metre. Even by the early 1970s, environments with steep slopes and/or rocks, such as canyons and seamounts, were very rarely sampled.

   Two notable innovations stimulated the next era of sampling in the deep sea. The development of the submersible *Alvin* and the movement of oil exploration into offshore waters led to the development of ROVs. With these two aids, sampling could be achieved at small scales and the sub-metre heterogeneity found at cold-water coral reefs, vents and cold seeps could be analysed. Many scientific sampling and analysis packages have been developed and deployed by submersibles and ROVs and with the fantastic improvement in position fixing through GPS, detailed photograph mosaicking of the seabed can occur. In addition, landers and long-term observatories have become an important tool in the armoury of the deep-sea ecologists. In the final analysis, however, there are still areas of the deep sea that are difficult to sample. Canyons with their steep sides, underhangs and strong currents remain a challenge, as do the ocean trenches. Deep-sea ecologists are also very aware of *their* sampling impact on the deep-sea bed and sampling strategy is now devised to cause the minimal amount of damage to the environment. Sampling technology will continue to develop at all scales within the deep sea, and include a focus on temporal variation. Already we are seeing the establishment of 'remote sensing' networks in the Northeast Pacific, and the use of AUVs, both of which will allow access from desk top to the deep sea without the need to board a ship!

Acknowledgements

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